

2022

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David A. Weber
University of Georgia

Evan P. Tanner
Caesar Kleberg Wildlife Research Institute

Theron M. Terhune II
Tall Timbers

J. Morgan Varner
Tall Timbers

James A. Martin
University of Georgia

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Recommended Citation

Weber, David A.; Tanner, Evan P.; Terhune, Theron M. II; Varner, J. Morgan; and Martin, James A. (2022) "Northern Bobwhite and Fire: A Review and Synthesis," *National Quail Symposium Proceedings*: Vol. 9 , Article 63.

<https://doi.org/10.7290/nqsp09V0ju>

Available at: <https://trace.tennessee.edu/nqsp/vol9/iss1/63>

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NORTHERN BOBWHITE AND PRESCRIBED FIRE: A REVIEW AND SYNTHESIS

David A. Weber¹

Warnell School of Forestry and Natural Resources, University of Georgia, 180 East Green Street, Athens, GA 30602, USA

Evan P. Tanner

Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA

Theron M. Terhune II²

Tall Timbers Research Station and Land Conservancy, 13093 Henry Beadel Drive, Tallahassee, FL 32312, USA

J. Morgan Varner

Tall Timbers Research Station and Land Conservancy, 13093 Henry Beadel Drive, Tallahassee, FL 32312, USA

James A. Martin

Warnell School of Forestry and Natural Resources, University of Georgia, 180 East Green Street, Athens, GA 30602, USA

ABSTRACT

Our understanding of the relationship between northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and fire began with Herbert Stoddard's work in the early 20th century. Research on the topic has continued, but our application of fire is deeply rooted in Stoddard's work, even as it has become evident that fire regimes must be adapted to variable environmental conditions that are evolving with a changing landscape and climate. A comprehensive review and synthesis of the literature on this topic would help formalize research advancements since Stoddard and identify knowledge gaps for future research. Results from experiments suggest fire creates favorable local habitat conditions for bobwhite such as plant composition, bare ground, and plant structure. Frequent prescribed fire is closely tied to where bobwhite populations are at their greatest (e.g., Red Hills region of Georgia and Florida, USA). However, an empirical gap exists between patch-level conditions and the bobwhite-landscape ecology interface. For example, it is well established that a 2-year fire return interval in pine savanna ecosystems with fertile soil is best for bobwhite. But causal evidence is limited for areas of different soil types, precipitation, and past land use across the bobwhite range. We review the extant literature describing prescribed fire use for bobwhite management, focusing on documented effects of fire on life-history characteristics of bobwhite under different environmental conditions. Habitat outcomes of fire management depend on fire frequency, seasonality, scale, and interaction with other management, and different strategies should be employed depending on the environment and desired effects. Adaptive management strategies will be necessary to address the challenges of rising temperatures associated with a changing climate, which are likely to alter the conditions under which burns occur and increase the difficulty of meeting basic burn criteria. Positive public attitudes toward prescribed fire will be key to developing a policy and management framework that supports efficient prescribed fire application. Our review elucidates range-wide processes and patterns to better inform the site-specific application of fire.

Citation: Weber, D. A., E. P. Tanner, T. M. Terhune II, J. M. Varner, and J. A. Martin. 2022. Northern bobwhite and prescribed fire: a review and synthesis. *National Quail Symposium Proceedings* 9:306–319. <https://doi.org/10.7290/nqsp09V0ju>

Key words: climate change, *Colinus virginianus*, Great Plains, habitat management, life history, northern bobwhite, pine savanna, policy

¹ E-mail: david.weber@uga.edu

² Present address: Orton Plantation Holdings, LLC, 9149 Orton Road SE, Winnabow, NC 28479, USA.

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The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has declined significantly throughout its range since at least the 1960s (Pardieck et al. 2020) and has likely declined in parts of its range since well before then (Stoddard 1931). Habitat loss and fragmentation associated with changes in land use, including plant succession, urbanization, and a shift toward agricultural and silvicultural practices that maximize commodity yield, have likely been the main drivers of this decline (Brennan 1991, Hernández et al. 2013). General bobwhite habitat requirements have been known for almost a century, and the use of fire has been well established as a tool to create and maintain a plant community favorable to bobwhite that includes a mixture of bare ground and grass, forb, and shrub cover (Stoddard 1931, Brennan et al. 1998, Cox and Widener 2008). Inconsistent and inappropriate application of prescribed fire, however, has hindered its efficacy in reversing bobwhite declines, making it paramount to build a common understanding of the relationship between bobwhite and prescribed fire throughout its range.

Bobwhite evolved in a pyrogenic ecosystem (Stoddard 1931). Prior to European settlement, lightning ignited fires across the bobwhite range as dry fuels accumulated or during periods of drought (Reid et al. 2010), maintaining grassland communities against encroaching woody species (Komarek 1965). Native American tribes used fire extensively to create landscapes for resource production, composing a mosaic of vegetation types and patches with different times since fire (Buckner 1989, DeVivo 1991, Pyne et al. 1996). Historical fire return intervals throughout much of the bobwhite range remained relatively frequent (i.e., 2–6 years; Guyette et al. 2012) until the early 1900s. It was then that government agencies attempted to ban fire use for forest protection and pine regeneration in the southeastern United States, while also suppressing fire in the Great Plains to limit risks to increasing human settlement. Moreover, increased grazing pressures that reduced fuel loads became common in the Great Plains (Fuhlendorf and Engle 2001), and decreased fire frequencies followed shifts in grazing management (Van Auken 2009). The reductions in burning in the early 20th century created conditions unsuitable for bobwhite, as the lack of fire or other disturbance allowed vegetation communities to shift to forest, resulting in a loss of food resources and cover and contributing to bobwhite declines (Brennan 1991). It was not until the 1940s and 1950s that prescribed burning for fuel reduction gained general acceptance (Pyne 1982). Since then, prescribed fire has been a common management strategy to promote bobwhite populations. However, there exists uncertainty among managers as to the optimal implementation of prescribed fire parameters across the bobwhite range.

Fire provides a multitude of benefits to bobwhite, most importantly creating habitat conditions that promote bobwhite food abundance and availability (Brennan et al. 2000), provide cover and diverse vegetation structure (Brennan et al. 1998), and increase ease of mobility (Carver et al. 2000, Cram et al. 2002). As a facultative grassland species that requires herbaceous vegetation with shrub components, bobwhite

depend upon intermittent disturbance to prevent encroachment of trees that outcompete annual and perennial herbaceous plants. Historically, periodic, low-intensity fire was the primary disturbing force across the bobwhite range (Pyne 1982). Fire reduces litter and can prevent canopy closure or excessive woody plant encroachment (Fuhlendorf and Engle 2001, Vander Yacht et al. 2017, Varner 2018) and is necessary to maintain open-canopy forest types in eastern forested systems and herbaceous components in rangelands of the Great Plains.

Prescribed fire frequency, timing, and size are all known to be important parameters affecting bobwhite habitat quality (Wellendorf and Palmer 2009, Kroeger et al. 2020). Fire frequency affects the heterogeneity of vegetation structure and composition and the degree to which woody plants may encroach on and shade herbaceous vegetation beneficial to bobwhite (Stoddard 1931, Brockway and Lewis 1997, Fuhlendorf and Engle 2001). In pine ecosystems, frequent fire (occurring every 1–2 years) promotes environments dominated by grasses and forbs (Streng et al. 1996, Glitzenstein et al. 2012), providing important nesting and brood cover for bobwhite (Brooke et al. 2017). Less frequent fire (occurring every 3–5 years) promotes a greater abundance of woody plants (Streng et al. 1996, Glitzenstein et al. 2012), which can provide escape cover (Cram et al. 2002, Brooke et al. 2017, Rosche 2018). The time at which prescribed fire occurs during the year relates to plant phenology and potentially fire intensity, thereby differentially affecting plant community composition and subsequently bobwhite habitat. Dormant-season burning tends to promote and maintain low woody cover, while growing-season fire tends to reduce woody species and stimulate diversity of the herbaceous understory (Boyer 1993, Drewa et al. 2002, Knapp et al. 2009). Burn size affects the degree of patch interspersion, and thus the distance bobwhite must travel to access different food and cover sources, and patch edge-to-interior ratios, which may influence predation dynamics (Wellendorf and Palmer 2009, Kamps et al. 2017, McGrath et al. 2017).

The effects of burn parameters on bobwhite are further complicated by the fact that bobwhite resource selection varies with life stage and spatial scale (McGrath et al. 2017). Some fire regimes will produce better food resources for chicks, whereas others may produce better cover for nesting. This important nuance helps us understand how bobwhite optimize resource selection when acquiring food and avoiding predators.

Prescribed fire alone may not be sufficient to achieve substantial long-term shifts in vegetation composition and structure. However, the effects of prescribed fire can be augmented or enhanced with complementary management actions. Grazing, herbicide, mechanical vegetation treatment, and other management tactics can all influence the impact of prescribed burning on bobwhite habitat. Managers must consider the frequency, timing, and type of application of each of these management strategies. However, there is limited cohesive information available on how different management strategies interact with prescribed burning to alter vegetation patterns in bobwhite habitat.

In addition to balancing fire frequency, timing, size, and interacting effects with other management strategies, managers must contend with effects of environmental conditions on fire impacts. For example, a fire return interval that is appropriate for mesic areas may be too frequent for xeric sites (Hardy 2003, Pausas and Keeley 2014, Rosche et al. 2019), and fire frequencies that produce herbaceous-dominated communities in Ultisol flatwoods have been shown to have little effect on shrub cover in Spodosol flatwoods (Glitzenstein et al. 2003). Appropriate fire regimes will thus vary regionally but have the objective of creating a mixture of herbaceous and woody cover, while limiting the woody stratum to avoid shading the understory (Rosche et al. 2019).

Despite the relatively common use of prescribed fire, overall efforts to reverse bobwhite declines have had limited success, although there have been isolated examples of bobwhite recovery through exceptional management, including appropriate use of prescribed fire (Sisson et al. 2012). Moreover, in much of the Great Plains, fire has been viewed as a tool rather than an ecological process (Fuhlendorf and Engle 2001). This approach has often led to homogenization of fire regimes (i.e., early intensive stocking of cattle) that reduces variation in fire frequency, fire extent, and fire severity, resulting in decreased habitat for bobwhite. Prescribed fire management may be operating at scales too large or too small relative to habitat patch size or too frequent or infrequent to alter plant communities optimally for bobwhite (Williams et al. 2004, Bowling et al. 2014). Furthermore, there are few cohesive recommendations on how fire management should vary according to regional environmental conditions and to meet the needs of bobwhite across their life cycle and spatial scales. We reviewed and synthesized the literature on how fire frequency, timing, size, and interactions with other management strategies influence bobwhite ecology and provide management recommendations for these parameters under differing environmental conditions.

METHODS

We sought and reviewed relevant studies using web search engines (e.g., Google Scholar) and targeted search terms (e.g., “bobwhite,” “fire,” “prescribed burn,” “habitat management,”) and reviewed studies cited in these papers. We also used our knowledge of the extant literature to augment the web search engines (e.g., recent theses and dissertations). We reviewed direct and indirect relationships between prescribed fire and bobwhite and provided generalized conclusions and recommendations for managers based on our findings. We categorized impacts according to 4 burn parameters that managers have most control over: fire frequency, fire timing, burn size, and interaction with other types of management. Understanding how these parameters affect bobwhite demographics and life history will allow bobwhite managers to make prescribed burning decisions that better meet their objectives. We reviewed the potential effects

of climate change on managers’ ability to conduct prescribed burns and the human dimensions influencing fire policy and public perception. Finally, we identified opportunities for future research and challenges facing prescribed fire use for bobwhite recovery.

RESULTS

Influence of Prescribed Fire on Bobwhite

Fire frequency in mesic environments.—Effects of fire frequency on bobwhite ecology vary with region and site productivity. Studies occurring in different regions, with different soil conditions, and targeting different bobwhite life stages have reported differing bobwhite habitat use and abundance patterns related to time since fire (Table 1). On private property in Georgetown County, South Carolina, USA, McGrath et al. (2017) found that bobwhite selected for areas with longer fire return intervals during winter (1 Dec–1 Mar) than during the breeding season (1 May–1 Oct; Table 1). Nonbrooding birds may prefer more cover as they search for nest sites, as nest sites are typically within areas of greater cover compared to the surrounding area (Lusk et al. 2006). McGrath et al. (2017) suggested that a 2-year fire return interval may provide a good balance for the cover-food resource optimization problem by promoting concealing vegetation for nests while still allowing ease of mobility and decreased visual obstruction for predator avoidance. This is consistent with findings from Dougherty and Baker counties, Georgia, USA that prescribed burning creates suitable cover conditions for nesting 1 and 2 years after fire (Simpson 1972). Similarly, at Avon Park Air Force Range in south-central Florida, USA, where primary plant communities include pine flatwoods, wet and dry prairies, and pine plantations, Miley and Lichtler (2009) reported that bobwhite abundance increased on sites that received a burn the previous year but decreased after 2 years post-burn (Table 1).

The dominant vegetation at a site influences habitat outcomes of prescribed fire frequency. Kroeger et al. (2020) suggest that the discrepancy between their findings of bobwhite selection for areas 1 year since fire and the findings of Cram et al. (2002) of selection for areas 3 years since fire (Table 1) is likely due to the dominance of different grasses. Wiregrass (*Aristida* spp.) in the Sandhills region of North Carolina, USA becomes matted to the point of restricting movement as time passes since last burn, whereas bluestems (*Andropogon* and *Schizachyrium* spp.) in Arkansas, USA remain upright after senescence and provide cover for multiple dormant seasons. Frequent burning in highly-productive mesic sites is likely necessary to keep diverse ground cover intact and viable, reduce woody stem density, and maintain bare ground (Moore 1972, Lewis and Harshbarger 1986, Hermann et al. 1998).

Frequent fire alone is enough to sustain shortleaf pine (*Pinus echinata*) and loblolly pine (*P. taeda*) woodland communities (Robertson et al. 2021). In these systems,

Table 1. Time since fire for which northern bobwhite (*Colinus virginianus*) show highest habitat use or abundance.

Study	Location	Parameter studied	Time since fire with greatest positive effect
Carroll et al. 2017a	Great Plains (OK)	Habitat use	No effect
Cram et al. 2002	Ouachita Mountains (AR)	Relative abundance	3 growing seasons
Kroeger et al. 2020	Sandhills (NC)	Nonbreeding habitat use	1 growing season or ≥ 3 growing seasons (if recent fire occurred in dormant season)
McGrath et al. 2017	Coastal Plain (SC)	Winter habitat use	2–3 years
McGrath et al. 2017	Coastal Plain (SC)	Breeding habitat use	1–2 years
Miley and Lichtler 2009	Coastal Plain (FL)	Abundance	1–2 years
Rosche 2018	Sandhills (NC)	Breeding habitat use	2 years
Rosche et al. 2019	Sandhills (NC)	Breeding habitat use	1–2 years
Sinnott et al. 2021	Central Plains (MO)	Brood habitat use	<2 years

fire return intervals of 1–2 years are likely necessary to maintain a fire-vegetation feedback loop, in which frequent fire promotes vegetation that creates more flammable fuels, namely pine litter and grasses (Beckage et al. 2009, Varner 2018, Robertson et al. 2019). However, loblolly-shortleaf pine communities may eventually transition to hardwood forest with fire return intervals >2–3 years (Matusick et al. 2020, Robertson et al. 2021). Under these longer return intervals, pine regeneration declines, likely because of excessive competition with other woody vegetation (Yocom 1972). The ensuing loss of flammable pine needle fuels would be expected to break the fire-vegetation feedback loop and allow for hardwood encroachment. Thus, under longer fire return intervals, these plant communities may transition to ones dominated by hardwoods or woody surface vegetation, which are inadequate for bobwhite (Brennan et al. 1998, Palmer and Sisson 2017, Robertson et al. 2021).

Fire frequency in xeric and semiarid environments.—Fire management should be adapted to site productivity and ultimate climatic conditions. Fire return intervals appropriate for mesic sites may be too frequent for xeric sites. Rosche (2018) found that bobwhite in the Sandhills region selected areas primarily 2 years after fire for nesting (Table 1). Thus, shortening fire return intervals to less than 3 years could increase the proportion of bobwhite nests exposed to fire and reduce nesting cover. At the microsite scale, bobwhite strongly select for areas with greater woody understory cover (Rosche et al. 2019, Kroeger et al. 2020). A 2- to 3-year fire return interval may be optimal for maintaining herbaceous groundcover, but it is too frequent to allow sufficient development of woody understory cover for bobwhite on unproductive sites (Kroeger et al. 2020).

Bobwhite response to prescribed fire varies along a gradient of soil productivity. In semiarid rangelands, bobwhite were found to have higher densities with early successional stages on more productive sites, whereas density was not affected by successional stage on less productive sites (Spears et al. 1993). Long et al. (2014) detected higher relative abundance of bobwhite in unburned patches compared

to 2-year and 4-year time-since-fire patches in a semiarid shortgrass prairie ecosystem in the panhandle of Texas, USA. Bobwhite should be considered a mid- to late successional species on less productive sites, and thus, fire management should be less aggressive in these areas (Spears et al. 1993).

In a sand shinnery oak (*Quercus havardii*) community in western Oklahoma, USA, prescribed fire applied across large portions of the landscape appeared to have minimal effect on bobwhite space use (Carroll et al. 2017a) and nest survival (Carroll et al. 2017b). Individuals were neither relatively attracted to nor repelled by different time-since-fire treatments, and there was no difference in spring dispersal movements among these treatments. These observations were similar to those of Ransom and Schulz (2007), who found little effect of fire on bobwhite density in Texas. However, Carroll et al. (2017a) reported that bobwhite coveys using burn treatments of 25–36 months post fire, which coincides with the time necessary for shinnery oak to recover to prefire structure (McIlvain 1954, Harrell et al. 2001), did exhibit smaller home range sizes compared to coveys using burn treatments of shorter or longer fire return intervals. Moreover, bobwhite exhibited reproductive plasticity in this system relative to time since fire. Nesting individuals would vary the dominant nesting substrate used depending on a patch's time since fire. In areas burned more recently (0–12 months since fire), nests were primarily located in shrubs, while a shift to herbaceous substrate occurred as time since fire increased (>36 months since fire). Though this shift in nesting substrate occurred due to changes in fire frequency, nest survival remained consistent across different time-since-fire patches (Carroll et al. 2017b). Overall, fire frequency may not have strong effects on bobwhite demographics in shinnery oak communities that exhibit rapid resprouting and structural recovery following fire.

Similarly, sand sagebrush (*Artemisia filifolia*) communities function as important areas for bobwhite in western rangelands (Tanner et al. 2015). This species has also been shown to exhibit rapid resprouting and structural recovery following fire. Plant height, canopy area, and canopy volume will return to unburned structural conditions 4 years post-fire, while plant

density remains the same 0.5–5 years post-fire compared to unburned patches (Winter et al. 2011).

These relationships between fire and vegetation response may not be consistent across the western fringe of the bobwhite range, where different types of vegetation may dominate. For example, lotebush (*Ziziphus obtusifolia*) is the primary source of fall, winter, and spring cover for bobwhite in the Rolling Plains region of West Texas (Renwald et al. 1978). However, once burned, lotebush may take 6–10 years to again become useful to bobwhite (Renwald et al. 1978). Thus, a frequent fire return interval in this region would be likely to eliminate important cover unless species like lotebush are protected from fire. However, direct management implications from other studies on bobwhite responses to prescribed fire in Oklahoma and Texas have not been definitive (Baumgartner 1946, Wilson and Crawford 1979, Carter et al. 2002, Ransom and Schulz 2007), and this area warrants further research.

Managers have virtually no control over soil moisture and water availability, yet these factors regularly influence the frequency of prescribed burning, especially on western rangelands. Successful burning depends on appropriate soil moisture conditions pre-burn and post-burn, and a lack of suitable conditions can restrict the burn window or eliminate it altogether. Damp soil is critical for protecting tree roots and microbes (Wade and Lundsford 1990). Burning under adequate soil moisture conditions may reduce damage to favorable plants for bobwhite, such as lotebush in the Rolling Plains of Texas (Renwald et al. 1978), or more effectively remove undesirable invasive plants, such as smooth brome (*Bromus inermis*; Blankespoor and Larson 1994). Managers seeking to reduce fire severity must also consider hydrologic conditions, as increased soil moisture has been shown to decrease heat transfer to soils (Badía et al. 2017).

Fire timing.—Here, we refer to “fire timing” as the period within the year that prescribed fire occurs. “Dormant season” refers to the period in which most plants are dormant, and “growing season” refers to the period during which most plants are actively growing. The timing of these seasons varies regionally. Lightning-ignited fires in the southeastern United States were historically common throughout the summer and peaked during May at the transition point between the dry spring and wet summer, when lightning incidence was at its highest (Knapp et al. 2009). Dormant-season fires were also common, likely the result of burning by Native Americans and early European colonists (Stambaugh et al. 2017). Prescribed burns in the Southeast on lands managed for bobwhite overwhelmingly occur during late dormant season or early growing season to avoid direct impacts on nesting birds, particularly bobwhite, and other wildlife (Knapp et al. 2009, Nowell et al. 2018). However, prescribed burns in the growing season (late spring and early summer) have increased in popularity as research has emerged demonstrating that this coincides with the historical period of lightning-ignited fire (Cox and Widener 2008). Fire timing may present unique challenges to managers, as the ability to burn depends on fuel loads and weather conditions. Managers of shortleaf

pine stands in Arkansas, for example, must contend with higher amounts of live fuels, lower amounts of fine (1 hour) fuels, lower total fuel loads, higher temperatures, and more unpredictable rainfall in the growing season compared to the dormant season (Sparks et al. 2002).

The primary differences in ecological effects of fire season are related to differences in fuel load, and thus fire intensity, and differences in plant phenology or growth stage at the time of fire (Knapp et al. 2009). In general, early growing-season burns tend to favor an understory with greater cover of grasses and forbs, whereas dormant-season burns favor sprouting of woody stems and shrubs (Boyer 1993, Brockway and Lewis 1997, Drewa et al. 2002, Knapp et al. 2009, Robertson and Hmielowski 2014). Studies at the Tall Timbers Research Station in Tallahassee, Florida, have found only subtle population-level effects of dormant-season versus growing-season burns on bobwhite (Brennan et al. 1998, 2000; Carver et al. 2000), but study authors acknowledge that much additional research is needed to fully understand long-term effects (Brennan et al. 2000). Fire timing in the context of wildlife management is certainly worth consideration as it affects bobwhite food resources, cover, and nesting success.

The timing of prescribed fire directly affects vegetation important to bobwhite for food provision. Brennan et al. (2000) found that sites burned in the growing season (May–Jun) produced more ragweed (*Ambrosia* spp.) and panicgrass (*Panicum* and *Dichanthelium* spp.), whereas sites burned during the dormant season (Feb–Mar) produced more legumes and oak (*Quercus* spp.) sprouts. Both ragweeds and panicgrasses are thought to be valuable plants for bobwhite, providing desirable food and structure for overhead cover (Korschgen 1948, Hurst 1972, Robel et al. 1979, Peters et al. 2015). Legumes, on the other hand, may provide enhanced forage quality over grasses due to their superior mix of essential amino acids (Peoples et al. 1994). Growing-season fire additionally produces greater insect prey abundance during brood-rearing months (Brennan et al. 2000). Availability of insects as a food resource is critical for bobwhite chick growth and survival (Nestler et al. 1942, Hurst 1972).

Fire timing also affects the availability of different components of cover for bobwhite. Dormant-season burns promote woody understory growth important for bobwhite cover. In the Sandhills region of North Carolina, Kroeger et al. (2020) found that bobwhite selected upland areas ≥ 3 growing seasons since fire if the recent fire occurred in the dormant season. Rosche et al. (2019) found that bobwhite selected for areas burned in the dormant season of the same year but avoided areas burned in the current growing season, likely because of a lack of woody understory important for escape, nesting, and thermal cover. This is congruent with the additional finding of Kroeger et al. (2020) that bobwhite selected upland areas 1 growing season since fire regardless of burn season. On oldfields in East Tennessee, USA, dormant-season fire increased coverage of native warm-season grass and decreased coverage of grass undesirable for bobwhite (Gruchy and Harper 2014), consistent with other studies conducted in the South

(Whitehead and McConnell 1980, Manley 1994). In central Florida, Miley and Lichtler (2009) reported marginally higher bobwhite abundance following dormant season burns than growing season burns. However, other studies report that early growing-season fires are more effective than dormant-season fire in promoting native grass and forb growth and creating bare ground to allow for effective bobwhite movement (Waldrop et al. 1987, Streng et al. 1993, Glitzenstein et al. 1995). Growing-season fires can also maintain desirable vegetation structure as much as 6 months longer than dormant season fires (Cox and Widener 2008).

In southern Texas where invasive grasses dominate many rangelands (Wied et al. 2020) indicative of bobwhite habitat, species such as buffelgrass (*Cenchrus ciliaris*) respond positively to dormant-season prescribed fires (Kuvlesky et al. 2002, Tjelmeland et al. 2008). Such herbaceous invasive species' responses to prescribed fire can reduce bobwhite habitat and present a novel challenge for managers when implementing prescribed fire management in semiarid rangelands within the bobwhite distribution. In cases such as these, additional management strategies are necessary to revegetate infested rangelands with native vegetation. Sequentially applying herbicide, prescribed fire, and reseeding with native plants has been shown to increase productivity on range sites (Masters and Nissen 1998). Fire timing is still critical in this integrative management approach. Fire should be applied when the undesirable plants are in their vegetative stage of development and are more vulnerable to fire and native vegetation is dormant.

There is some risk of nest destruction during growing-season fires. The specific month during which burning occurs is important because bobwhite nesting varies significantly across the growing season. On Fort Bragg in North Carolina, Rosche (2018) documented 2 nests (6.7%) burned by prescribed fire during June and July. Twenty-three documented nests (77%) were located within units that were burned at least 2 years prior, putting them at greater risk of being destroyed by prescribed fire occurring on a return interval shorter than 3 years. The risk of nest destruction by fire was approximately proportional to the percentage of study area burned during the nesting season. Similarly, Martin (2010) found that dormant-season fires had positive effects on nest survival compared to growing-season fires, which resulted in direct nest losses. Fires conducted during the growing season may also reduce the area of available nesting habitat and increase predator search efficiency. Interestingly, both dormant season and growing season fires produced better outcomes on nest survival than no fire. Rosche et al. (2021), on the other hand, found that early growing-season (Apr–May) prescribed fire posed relatively low risk to bobwhite nests on Fort Bragg. In their study, most nests were in 2-year-old rough not scheduled to be burned on a predominantly 3-year fire return interval, and thus were not at risk of destruction from prescribed burning. A more frequent fire return interval would be likely to put nests at greater risk of destruction in this area. However, the authors note that nest site selection in relation to time

since fire varies with soil productivity. For example, a 2-year fire return interval would pose less risk to bobwhite in areas with high soil productivity, where bobwhite commonly nest in 0- or 1-year time-since fire areas (Simpson 1972). Other studies have shown few strong effects of fire timing on direct mortality, breeding success, or survival of birds (Engstrom et al. 1996, Cox and Widener 2008, Carroll et al. 2017b). As managers experiment with varying seasonality of burning, future research should evaluate direct and indirect effects on bobwhite habitat suitability.

Burn size.—The size of a prescribed burn influences bobwhite ecology through its effects on total area of a landscape burned, the ratio of burn edge to interior, which decreases as burn size increases, and the amount of resource interspersed, which also decreases as burn size increases. Wellendorf and Palmer (2009) reported that when comparing burn sizes of approximately 2.25 ha and 8 ha, smaller fires were associated with higher nest production, greater bobwhite autumn density, and lower risk of mortality in some years but not in others. Similarly, Martin (2010) found that for experimental burn sizes of 10 ha, 20 ha, and 40 ha, bobwhite densities were consistently greatest on plots with smaller fires. Martin (2010) proposed that foraging bobwhite may have greater difficulty escaping from avian predators on larger burn patches where postfire cover is sparse. Furthermore, the smallest fire size treatment in the study produced more chicks per hen than the 2 larger treatments.

In line with these two studies, McGrath et al. (2017) found selection patterns for smaller burn sizes. For the burn sizes observed in their study, odds of use for nonbrooding bobwhite increased linearly by 1.8 times for every 15.7-ha reduction in burn size (95% credible interval [CrI] = 1.7–1.9). Brooding birds also selected for areas with decreasing burn sizes at the second-order scale. However, at the third-order scale, brooding birds showed the highest selection for mid-range burn sizes (~79 ha). The authors suggest that as burn size increases, bobwhite food availability may increase while ability to avoid predators may decrease. Their findings could support the notion that bobwhite optimize habitat selection based on predator avoidance and food availability.

Larger burn sizes (>80 ha) appear to have mixed effects on bobwhite. Comparing average burn sizes of 85.87 ha and 1220.10 ha on a property consisting mostly of prairie and pine flatwoods, Kamps et al. (2017) found that apparent chick survival was positively correlated with amount of home range burned during the previous dormant season. Burned area also had an indirect positive effect on chick growth by reducing home range size. The authors attributed these findings to greater invertebrate abundance in areas with larger burns, but they did not measure invertebrate abundance. However, there may be tradeoffs between chick survival and adult survival. Kamps (2015) reported that as fire size increased, larger portions of individual bobwhite home ranges were burned, leading to increased movement and a reduction in adult survival. Miley and Lichtler (2009) found that bobwhite abundance increased more after larger fires (where at least

40% of an area was burned) than smaller fires. However, they did not investigate the effects of differing burn patch sizes for a consistent proportion of area burned. Further research should quantify how variable burn sizes affect bobwhite movement, food availability, and predation at different scales to better understand if and how these factors drive differences in bobwhite demographics and habitat selection patterns. The ratio of burn size to overall amount of habitat should also be investigated. We hypothesize that optimal individual fire sizes for bobwhite should be scaled to overall habitat amount. Quantifying the scalar function is an opportunity for future research.

Bobwhite response to different burn sizes is likely to vary regionally and by dominant vegetation type. In a sand shinnery oak community in western Oklahoma, landscape-scale fire had limited effects on short-term bobwhite movement and space use (Carroll et al. 2017a). Moreover, in a sand sagebrush community in western Oklahoma, bobwhite density was not shown to be different in pastures (406–848 ha) managed with patch-burn grazing compared to unburned, seasonal grazing (Holcomb et al. 2014). Similarly, burn sizes ranging from 57.1–109.7 ha had limited effects on bobwhite covey space use within the Rolling Plains of Texas, if residual woody plant species (primarily lotebush) remained present within the burn patches (Renwald et al. 1978). However, when coupled with grazing practices (i.e., pyric herbivory), positive responses in bobwhite densities have been shown to occur with burns ranging from 0.1–3.9 ha in size within semiarid rangelands, likely due to increases in vegetation heterogeneity (Grahmann et al. 2018). Rangelands within the western portion of the bobwhite distribution evolved with fire as an ecological process to maintain certain stable states and vegetation communities (Boyd and Bidwell 2001, Fuhlendorf and Engle 2001). Even within the context of extreme values of fire patch size in these rangelands (e.g., the East Amarillo Complex Wildfire [~367,000 ha]), there was little evidence to suggest any demographic response to this large fire patch size, and space use changed only marginally (Warren 2014). In general, it is likely that behavioral plasticity allows bobwhite to adapt to changing habitat conditions related to fire events, even across a wide range of fire patch sizes in western rangelands (Carroll et al. 2017b).

It is important to note that practical resource constraints may limit the flexibility managers have in applying fine-scale prescribed fire. For example, the average prescribed burn size on public lands from observations in the Federal Wildland Fire Occurrence database (Goodman 2016) is 226 ha (standard deviation = 839 ha; Mason and Lashley 2021), meaning many burns occur on a scale significantly larger than that investigated by most of the studies discussed in this review. Practitioners are limited by equipment, time, and personnel, and thus may be forced to burn at the largest, most efficient scales possible, and to burn adjacent blocks concurrently (Mason and Lashley 2021). While managers with ample resources often burn at much smaller scales on private lands where quail is a priority, more research is warranted to assist public land managers and

others in finding ways to cost effectively apply prescribed fire at finer scales appropriate for bobwhite.

Interaction of prescribed fire and other management.— Prescribed burning has interacting effects with other management strategies on bobwhite ecology. When used appropriately, herbicide application, grazing, mechanical vegetation treatment, and reseeding have the potential to enhance or complement the effects of prescribed burning on bobwhite habitat. On native grassland and intensively managed sites in southwestern Missouri, USA, for instance, bobwhite showed stronger selection for sites that were grazed and burned within 2 years relative to sites that were only grazed or only burned (Sinnott et al. 2021). Coupling grazing and burning promotes greater heterogeneity of vegetation composition and structure on grasslands. A shifting mosaic emerges as more intensive grazing occurs on certain patches of a burned area, and new burns further change the landscape (Fuhlendorf and Engle 2004, Veen et al. 2008, Grahmann et al. 2018). Sinnott et al. (2021) proposed that these heterogeneous, diverse prairie plant communities facilitate brood use through their provisioning of adequate cover, bare ground, and abundant invertebrates, which benefit juvenile foraging, growth, mobility, and survival (Hurst 1972, Taylor et al. 1999, Kamps et al. 2017). Grazing under appropriate stocking densities in conjunction with prescribed burning may also be used to effectively manage monotypic nonnative grasslands for bobwhite in semiarid environments by maintaining pressure on aggressively growing plants like bunchgrasses (e.g., *Cenchrus ciliaris*; Grahmann et al. 2018).

Although frequent prescribed burning alone may be sufficient to sustain shortleaf and loblolly pine communities (Robertson et al. 2021), additional management strategies are often necessary to maintain open-canopy forests to compensate for external constraints on the timing and frequency of prescribed fire and land use histories (Bragg et al. 2020). These strategies include timber management (Mitchell et al. 2006), mechanical and chemical treatment of understory vegetation (Welch et al. 2004, Burke et al. 2008), or planting and fertilizing native species (Knapp et al. 2011). Timber density may vary significantly even under consistent fire applications, and this variation has a relatively large effect on bobwhite abundance (Little et al. 2009). Therefore, reducing canopy coverage of timber and frequent prescribed fire may both be necessary to maintain or restore bobwhite populations.

In areas of severe hardwood encroachment, a one-time application of herbicide in conjunction with post-spray burning may be the most effective means of restoring suitable bobwhite habitat, as hardwoods recover quickly via root or collar sprouting after mechanical treatment alone (Welch et al. 2004, Burke et al. 2008). However, the choice of when to burn post-spray should be carefully considered because burning too soon may limit fuels and make pine regeneration difficult to control.

In western rangelands where invasive grasses are of particular concern, herbicide and reseeding may be used in

conjunction with fire to reduce the dominance of invasive plants. Application of herbicide followed by prescribed burning and seeding with warm-season grasses has been shown to reduce biomass of invasive grasses such as smooth brome and leafy spurge (*Euphorbia esula*) while increasing grass species richness, relative to no treatment (Masters and Nissen 1998, Link et al. 2017). Applying glyphosate before burning and seeding was significantly more effective at reducing smooth brome biomass than burning and seeding alone (Link et al. 2017). Overall, the effects of prescribed fire may be augmented, enhanced, or suppressed in conjunction with other management strategies, and the full range of management tools should be considered to meet objectives.

Implications of Global Climate Change on Bobwhite Management and Fire

Historically, variation in weather and climate have impacted bobwhite and other wildlife in several ways. Weather cycles and their effects on bobwhite have been studied and are known to vary regionally (Lusk et al. 2001). In the southwestern portion of the bobwhite range, for example, alternating wet and dry year cycles associated with the El Niño Southern Oscillation (ENSO) and dynamic fuel loads account for the bulk of interannual variability in the amount of area burned (Ryan et al. 2013). In the Southeast, however, where fuels are abundant, fire plays a major role in maintaining vegetation conditions conducive to bobwhite, but changes in fire extent and wildfire risk are also linked to the ENSO cycle (Brenner 1991, Chiodi et al. 2018). During La Niña years, the Southeast experiences reduced precipitation, which can increase fire risk, whereas El Niño years typically bring above-average precipitation and a reduced fire risk. This, in turn, impacts the interaction of vegetation conditions, predator-prey dynamics, and management prescriptions. Despite long-term management under these stochastic weather conditions, climate change presents added challenges to resource management due to its directionality and potential to influence the extent, duration, and intensity of weather patterns (Kupfer et al. 2020). Climate change is generally expected to create warmer, drier conditions in the west-southwest portion of the bobwhite range (Guyette et al. 2014), resulting in increased droughts. Meanwhile, warmer, wetter conditions are expected in parts of the Southeast (Guyette et al. 2014), resulting in more intense weather events (e.g., hurricanes, rainfall). These challenges hit at the heart of fire application and bobwhite management in multiple ways.

Investigations conducted by the Intergovernmental Panel on Climate Change (IPCC 2021) suggest that a heightened integration of climate change adaptation strategies into resource management is warranted for preserving ecosystem integrity and conserving species. Given that bobwhite are so tightly linked to fire, the need to assess the role that climate change might have on their future conservation and management is apparent. We lack an understanding of the inherent risk and extent of potential impacts of climate change on bobwhite. As such, we must be intentional in our approach to research into

fire effects on vegetation and bobwhite germane to climate change as well as be prescriptive and objective-oriented in our approach to management. At this point we know some of the ways that climate change will influence bobwhite as it relates to changing fire conditions.

Ecosystem function is influenced by the intersection of climate, management timing, and vegetation response. The role of fire in shaping vegetation is critical, yet regionally variable and contingent on edaphic conditions and precipitation. Given that prescribed burns require the proper alignment of time, resources, and suitable weather conditions, changing climate will unequivocally alter the effectiveness of fire and fuel management; accordingly, we must adapt how we manage fire and fuels (Kupfer et al. 2020, Gao et al. 2021).

The application of prescribed fire in the future does not come without challenges. Escalating temperatures will change fire regimes and our application of controlled burns as lower soil and fuel moisture will result in longer fire seasons and increased fire risk (Mitchell et al. 2014, Kupfer et al. 2020, Gao et al. 2021). Kupfer et al. (2020) contended that the practical constraints of rising temperatures on prescribed burning activity present a significant challenge and suggested that meeting basic burn criteria will become increasingly difficult over time. Furthermore, the warmer conditions are expected to increase wildfire frequency, intensity, and extent throughout much of the landscape (Price and Rind 1994, Gillett et al. 2006, Gao et al. 2021), presenting an additional challenge to prescribed fire activity. Moreover, increases in unprecedented droughts are projected over the next century within the American Southwest and central Great Plains (Cook et al. 2015). Wildfire activity is generally expected to increase in response to changing temperature and precipitation patterns within the bobwhite distribution, though this pattern will vary across the distribution (Liu et al. 2013, Guyette et al. 2014). Variability in drought conditions is also predicted to increase in North America (Cook et al. 2019). Decreases in fuel loads due to drought conditions can occur (Brown et al. 2005), making implementation of prescribed fire difficult in already semiarid systems. Moreover, within the southern Great Plains, wildfire activity is greatest after average or above-average precipitation conditions followed by drought conditions (Scasta et al. 2016), illustrating the challenges that drought variability may create for fire management.

Given the less desirable and less predictable weather conditions associated with climate change, land managers are projected to have fewer opportunities to conduct prescribed burns in the United States. For instance, recent research indicates that in some areas of the Southeast, fewer than 10–15% of summer days will remain viable for conducting prescribed burns by the end of the century under the most severe climate change projections (Kupfer et al. 2020). Those remaining available burn days in the growing season are expected to be more variable and less predictable, making it more difficult for resource managers to prepare and plan (Kupfer et al. 2020). As the likelihood of severe droughts amplifies wildfire occurrence and simultaneously restricts

burning opportunities, we can expect heightened public apprehension about prescribed fire and increased scrutiny for degradation of air quality when burns are conducted.

Despite the unknowns surrounding climate change effects, applying an adaptive management approach to changing fire regimes will help reduce ecosystem vulnerabilities and promote desirable conditions for bobwhite (Millar et al. 2007, Joyce et al. 2009). Taking advantage of prescribed fire in conjunction with other management practices (e.g., supplemental feeding, predator control) may buffer bobwhite populations during poor years and harsh conditions (e.g., inclement weather) and overcome shortfalls in prescribed fire application due to changing fire conditions from year to year. As the climate in the bobwhite range changes, research that captures how extremes influence fire application, habitat responses, and bobwhite life history should be prioritized.

Human Dimensions of Prescribed Fire

Continued use of prescribed fire in bobwhite management is contingent on public policies and regulations across the bobwhite range. Most of the states encompassing the bobwhite range have substantial prescribed fire programs, supported by state policies that encourage prescribed fire via reducing liability for burners, “Right to Farm” legislation supporting prescribed burning as a land use right, and state and federal programs that aid landowners (Brennan et al. 1998, Burger et al. 2006, Ryan et al. 2013). Challenges remain for the continued use of prescribed fire, however. Social acceptance for prescribed fire is surprisingly strong (studies report >79% public acceptance across the United States; McCaffrey 2006, Polo et al. 2020). This acceptance varies across the bobwhite range, with high acceptance in many rural communities near prescribed burns where habitat is also most prioritized. Escaped prescribed fires, smoke incidents in cities and on major highways, and greenhouse gas regulations all have the potential to reduce public support and erode state and federal protections. The engagement of bobwhite advocacy and management groups offers some promise to maintain support for prescribed fire.

Prescribed burn associations (PBAs) are increasing throughout much of the bobwhite’s western distribution in the southern Great Plains and are crucial to providing information about prescribed fire and facilitating prescribed burning activity on private rangelands (Toledo et al. 2014). Lack of training and lack of equipment are 2 common reasons why private landowners in western rangelands decide not to use prescribed fire as a management tool (Polo et al. 2020). The local land managers and private landowners who make up the PBAs work together to promote and provide support for local prescribed fire activity and offer a unique social construct for continuing prescribed fire practices in parts of the bobwhite distribution. An example, the Edwards Plateau Prescribed Burn Association in Texas, which started in 1997, now has >300 members and works on >150,000 ha as of 2015 (Twidwell et al. 2013). Belonging to a PBA is a strong predictor of whether a landowner has an increased probability of using prescribed fire in these rangelands (Stroman et al. 2020). These associations will continue to be an

important catalyst for implementation of prescribed fire in the western portion of the bobwhite distribution.

Challenges and Research Needs

Further research is needed to comprehensively understand the effects of prescribed fire on bobwhite ecology and how these effects vary across the bobwhite range (Table 2). Almost no research has been done outside of the historical longleaf pine (*Pinus palustris*) range or the rangelands of the Great Plains. The ideal fire return interval will vary by region, and more research is needed to understand what interval is best for what area. Similarly, it is unclear how fire timing should vary across the bobwhite range. More research is also needed to better understand the effects of different burn sizes at different management scales on bobwhite demographics. Researchers should quantify how burn size at different scales affects invertebrate prey abundance and predation risk, but more importantly, how fire size, timing, and frequency interact to affect bobwhite demography.

Rising temperatures associated with climate change may pose practical constraints on fire activities. Adaptive management strategies will be needed to prepare for a future in which meeting basic burn criteria becomes increasingly difficult, especially during the growing season (Kupfer et al. 2020). Moreover, research on the effects of prescribed fire on thermal landscapes is largely lacking (Elmore et al. 2017). As discussed earlier, fire alters the vegetation structure and composition within a patch, which in turn will alter the thermal landscape (Anthony et al. 2020, Londe et al. 2020) and may reduce thermal refuges under changing climate scenarios. Linking climate-change induced effects on bobwhite life history to challenges and restrictions on prescribed fire will be critical to long-term conservation of bobwhite populations.

Finally, necessary policy changes to allow for efficient and

Table 2. Research needs for northern bobwhite (*Colinus virginianus*) in relation to prescribed fire.

Research question or project
A manipulative experiment to address range-wide variation in fire frequency, fire season, and burn timing. Ideally, the experiment would explore the interactive effects of each factor.
What are the impacts of exotic and invasive plants on fire management for bobwhite?
How does prescribed fire interact with other disturbances and land uses such as grazing?
How does the future climate-constrained burn window affect plant communities and bobwhite demography?
What are the tradeoffs among fire surrogates such as mechanical treatments, herbicides, and grazing for bobwhite habitat demography?
What are the direct and indirect effects of prescribed fire on the spatial and population ecology of the masked bobwhite (<i>Colinus virginianus ridgwayi</i>), and how can these relationships help guide future recovery plans?

appropriate fire management must be identified. Prescribed fire is a necessary element to bobwhite management and a tremendous diversity of other animals and plants within the bobwhite distribution (Brennan et al. 1998, Engstrom and Palmer 2005). Prescribed fire policies and regulations are state based, so the diversity of challenges within the native bobwhite range will be great. Restrictions on burning near the wildland-urban interface and in areas with limited prescribed fire windows will be a major challenge in long-term conservation efforts (Ryan et al. 2013). Looking beyond overcoming burn restrictions, there exists an emerging opportunity to increase prescribed fire through new state and federal policies which will increase funding for prescribed fire, fire training, and fire education as well as mechanical treatments to mitigate wildfire risks. Given the importance of fire to bobwhite, policy synthesis and additional research are urgently needed to ensure that conservation of species is included in fire policy outcomes.

To overcome uncertainty surrounding prescribed burning, developing invigorated decision-support tools that allow for better prediction of smoke transport and ensuring safety should be prioritized (Hiers et al. 2020). Moreover, prescribed burn associations offer an important platform for working collectively to provide support for prescribed fire implementation (Toledo et al. 2014, Polo et al. 2020). Last, engagement between wildlife biologists and fire managers with state and federal regulators should be emphasized to better integrate the latest science with pragmatic application of fire.

MANAGEMENT IMPLICATIONS

Prescribed fire managers charged with considering bobwhite objectives have several critical variables to consider when planning burns—fire frequency, fire timing, burn size, and interactions with other management—in addition to the essential safety precautions. Our implications assume bobwhite are the primary objective while recognizing that other objectives and constraints exist. Principally, the ideal fire regime to maximize bobwhite populations maintains a plant community dominated by forbs (>50%), moderate grass cover (25–50%), 15–30% shrub cover, and minimal litter on the ground. Thus, managers must balance burning frequently enough to create and maintain the aforementioned plant community without removing so much cover as to negatively affect survival. Local conditions should dictate the optimal fire frequency, timing, and scale; however, we offer some best management practices to achieve suitable bobwhite habitat. A 2-year fire return interval is ideal on mesic sites in temperate climate zones, especially in the presence of aggressive tree species such as sweetgum (*Liquidambar styraciflua*); otherwise, a midstory develops that rapidly reduces bobwhite habitat. On sandhill sites or other xeric environments that lack a strong invasive tree component, an average return interval of 3 years, with some areas allowed to go 4–5 years between burns to allow for development of shrub cover, may create favorable conditions. In semiarid or arid environments, even longer fire return intervals may be

warranted to allow important native food and cover plants to recover. In the maintenance phase of management (i.e., bobwhite population meeting target density), prescribed fire should occur during the late dormant through the early growing season. Pulses in predatory hawk populations during migration should be a consideration for burn timing (Rectenwald et al. 2021). We recommend altering the seasonality of burns across years for a given burn unit and spatially among burn units within years to minimize the homogenization of vegetation. During restoration, burning outside this window to reduce fuels and kill hardwoods is acceptable. Outside of western rangelands where fire size has limited effects on bobwhite, individual fire sizes should be the smallest possible given operational constraints. The composition of the landscape should be a mosaic of recent burns and less recent burns such that any given point on the landscape is proximal to multiple seral stages. Other management strategies (e.g., herbicide, grazing, mechanical treatment, reseeded) should be integrated with fire management when appropriate to achieve desired vegetation outcomes.

Climate change will affect bobwhite and other wildlife. Learning to adapt to this new reality, mitigating risks associated with wildfires, and overcoming impediments to implementation of prescribed burns will require intentional, decisive action from policy makers and resource managers. Operationally, the main threat to prescribed fire use for bobwhite is the shrinking burn window. Thus, we recommend establishing habitat cooperatives among well-managed private and public lands to maintain or increase burned area in the face of climate change.

ACKNOWLEDGMENTS

We will always be indebted to H.L. Stoddard for his dedication to bobwhite and fire ecology. This research would not be possible without support through The Robert C. Balfour Game Bird Management Fellowship, Gerry Game Bird Endowment, and Pamela H. Firman Quail Management Research Initiative at Tall Timbers. This work was also funded by McIntire-Stennis project 1012498.

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