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Author: Behney, Adam C.

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## RESEARCH ARTICLE

# High-intensity short-duration grazing during spring is not an effective habitat management tool for Northern Bobwhites in Colorado

Adam C. Behney\*,<sup>ORCID</sup>

Avian Research Section, Colorado Parks and Wildlife, Fort Collins, Colorado, USA

\*Corresponding author: [adam.behney@state.co.us](mailto:adam.behney@state.co.us)

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**ABSTRACT**

Many wildlife species, like Northern Bobwhite (*Colinus virginianus*), are reliant on periodic environmental disturbance to maintain heterogeneity in vegetation patterns. The Northern Bobwhite is a species of conservation concern requiring different vegetation types for nesting and brood-rearing stages, as well as for protection from predators and extreme weather. In northeastern Colorado, there are few management options to increase disturbance, other than domestic livestock grazing, to manage Northern Bobwhite habitat. As high-intensity short-duration grazing has shown promise as a mode of disturbance to manage Northern Bobwhite habitat in other regions, I used a randomized block design to test the effect of spring high-intensity short-duration grazing on Northern Bobwhites and their habitat in northeastern Colorado from 2016 to 2019. Specifically, I monitored Northern Bobwhite nest and brood survival and habitat selection in relation to grazing treatments over 3 years. I found that grazing had no effect on nest or brood survival or brood habitat selection, but Northern Bobwhites selected against grazed plots for nesting. Nest survival was negatively influenced by percent litter around the nest, and Northern Bobwhites selected nest sites with more grass cover and less bare ground. Broods selected habitat with less bare ground and more woody vegetation. Grazing affected vegetation immediately after grazing, but these effects weakened or disappeared by the end of the growing season. One exception to this overall pattern was forbs, which tended to be more abundant on grazed plots throughout the growing season. Overall, I found neutral effects of grazing on Northern Bobwhite nest and brood survival and habitat selection and neutral to positive benefits to the vegetation. Spring high-intensity short-duration grazing does not appear to be an effective tool to manage Northern Bobwhite nest or brood habitat in northeastern Colorado.

**Keywords:** Bayesian, breeding ecology, brood success, *Colinus virginianus*, disturbance, grazing, habitat selection, nest success

**LAY SUMMARY**

- Northern Bobwhite populations have experienced range-wide declines and in Colorado, it was thought that declines were due to lack of vegetation disturbance.
- I tested whether grazing with a high cattle density for a short period in the spring could improve Northern Bobwhite habitat. The primary focus was on improving foraging and brood-rearing habitat by creating more bare ground and forb coverage.
- Grazing had no influence on brood habitat selection, brood survival, or nest survival; however, Northern Bobwhites selected ungrazed areas for nesting.
- Vegetation was substantially impacted directly after spring grazing, but by the end of the growing season, there was little to no difference in vegetation measurements between grazed and ungrazed areas.
- Overall, spring high-intensity short-duration grazing does not appear to be an effective habitat management strategy for Northern Bobwhites in northeastern Colorado because it did not result in any positive response of broods and grazed areas were avoided for nests.

**El pastoreo de alta intensidad y corta duración durante la primavera no es una herramienta de manejo de hábitat efectiva para *Colinus virginianus* en Colorado****RESUMEN**

Muchas especies de vida silvestre, como *Colinus virginianus*, son dependientes de disturbios ambientales para mantener la heterogeneidad en los patrones de vegetación. *C. virginianus* es una especie de preocupación para la conservación que requiere diferentes tipos de vegetación para las etapas de anidación y cría de la nidada, así como para protegerse de los depredadores y del clima extremo. En el noreste de Colorado hay unas pocas opciones

de manejo para aumentar el disturbio, más allá del pastoreo por el ganado doméstico, para manejar el hábitat de *C. virginianus*. Así como el pastoreo de alta intensidad y corta duración se ha mostrado prometedor como un modo de disturbio para manejar el hábitat de *C. virginianus* en otras regiones, usé un diseño en bloque aleatorizado para evaluar el efecto del pastoreo de primavera de alta intensidad y corta duración sobre *C. virginianus* y su hábitat en el noreste de Colorado desde 2016 hasta 2019. Específicamente, monitoreé la supervivencia del nido y de las crías y la selección de hábitat en relación al tratamiento de pastoreo a lo largo de 3 años. Encontré que el pastoreo no tuvo un efecto sobre la supervivencia del nido y de las crías o sobre la selección de hábitat de las crías, pero que *C. virginianus* evitó parcelas pastoreadas para anidar. La supervivencia del nido estuvo negativamente influenciada por el porcentaje de hojarasca alrededor del nido, y *C. virginianus* seleccionó sitios de anidación con más cobertura de pastos y menos suelo desnudo. Las crías seleccionaron hábitat con menos suelo desnudo y más vegetación leñosa. El pastoreo afectó la vegetación inmediatamente después del pastoreo, pero estos efectos se debilitaron o desaparecieron hacia fines de la estación de crecimiento. Una excepción a este patrón general fueron las forbias, que tendieron a ser más abundantes en las parcelas pastoreadas a lo largo de la estación de crecimiento. En general, encontré efectos neutros del pastoreo sobre la supervivencia del nido y de las crías y sobre la selección de hábitat de *C. virginianus*, y beneficios neutros a positivos para la vegetación. El pastoreo de primavera de alta intensidad y corta duración no parece ser una herramienta de manejo efectiva del hábitat del nido o de las crías de *C. virginianus* en el noreste de Colorado.

**Palabras clave:** Bayesiano, *Colinus virginianus*, disturbio, ecología de la cría, éxito del nido, pastoreo, selección de hábitat

## INTRODUCTION

Widespread suppression of natural disturbances from wildfire, flooding, and grazing by native herbivores has reduced vegetation heterogeneity in many prairie ecosystems (Knapp et al. 1999, Fuhlendorf et al. 2017). Vegetation heterogeneity is essential, however, for meeting the different requirements of various activities and life-stages for many wildlife species (Kie et al. 2002, Hagen et al. 2004, Brennan and Kuvlesky 2005). Without periodic disturbance, grasses or other vegetation may become too dense with little bare ground (McCoy et al. 2001), precluding use by certain species of wildlife such as the Northern Bobwhite (*Colinus virginianus*; hereafter bobwhite; Klimstra and Ziccardi 1963, Hammerquist-Wilson and Crawford 1981). Therefore, managers periodically disturb vegetation to maintain the availability of different seral stages through methods like burning, disking, mowing, or grazing.

Domestic livestock grazing, primarily by cattle, is one of the most common land-use practices in western North America (Fleischner 1994, Bigelow and Borchers 2017); and controlled grazing in which pastures are grazed and then allowed to rest can be a valuable tool to increase habitat heterogeneity for bobwhites (Holechek et al. 1982). In contrast, unmanaged continuous grazing in which pastures are grazed constantly with no rest at stocking rates that are too high for vegetation recovery has caused substantial grassland degradation throughout western North America (Fleischner 1994). Controlled grazing may be the only viable option to create disturbance in areas where the terrain (e.g., steep slopes, soft soils, and obstructions like standing trees and deadfall) does not permit access by machinery or restrictions preclude the use of prescribed fire (Quinn-Davidson and Varner 2012). One form of controlled grazing, high-intensity short-duration grazing,

is a system in which pastures are grazed at high stocking rates for short periods (e.g., 5 days grazed followed by 7 weeks ungrazed; Holechek 1983). This system has been shown to have positive effects on bobwhites and their habitat (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992). High cattle densities for short periods of time can increase water infiltration of the soil due to hoof action, reduce forage selectivity of cattle, improve leaf area index, and support a more even effect of grazing within each pasture (Holechek 1983), which likely contributed to the reported positive effects on bobwhite habitat.

Bobwhite populations have declined across the majority of their range, due primarily to the loss or conversion of suitable habitat (Brennan 1991, Brennan and Kuvlesky 2005, Hernandez et al. 2013, Sauer et al. 2017). Bobwhites require a diversity of vegetation types to satisfy the needs of various life-stages: areas with woody cover for resting and protection from predators and harsh weather, areas with forbs and bare ground for feeding and brood-rearing, and areas with grass for nesting (Snyder 1978, Taylor et al. 1999, Perkins et al. 2014). Compared with less intense grazing systems, high-intensity short-duration grazing creates more bare ground and less dense grass (Hammerquist-Wilson and Crawford 1981), which may improve bobwhite foraging and brooding habitat (Taylor et al. 1999). Alternatively, Lusk et al. (2001) predicted that bobwhite counts would decrease as cattle density increased, but their model did not consider grazing duration nor did it focus specifically on foraging or brooding habitat. Although high-intensity short-duration grazing has shown promise in areas like south Texas (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992), these results should be applied cautiously or tested in

regions that differ in climate, growing season, soil conditions, and other factors that may affect plant response to grazing (Spears et al. 1993).

Colorado lies at the northwestern edge of the bobwhite range (Brennan et al. 2020). In northeast Colorado, bobwhites are generally limited to river-bottom riparian areas where there is sufficient woody cover (Snyder 1978). Bobwhites are a popular gamebird and during the 2012–2013 hunting season; for example, ~965 hunters harvested 5,212 birds in Colorado (Colorado Parks and Wildlife 2013). Due to bobwhites' restricted range in Colorado and a goal of maintaining or increasing huntable populations, managers wish to conduct habitat management that will facilitate population sustainability or growth and range expansion. Little information exists on optimal habitat management strategies for bobwhites in river-bottom riparian areas such as those found in northeastern Colorado, and most of it is focused on habitat management during winter (Snyder 1978) rather than during the nesting or brood-rearing seasons.

Given the knowledge gap regarding habitat management strategies in the forested riparian area that bobwhites occupy in northeastern Colorado, and limitations associated with other methods of disturbance in this area (steep slopes, soft soils, and obstructions like standing trees and deadfall), I assessed whether high-intensity short-duration grazing could be used as a mode of disturbance to improve breeding habitat. I monitored bobwhite nest and brood survival and habitat selection as well as vegetation characteristics in relation to grazing treatments on a large state wildlife area in northeastern Colorado from 2016 to 2019. My specific objectives were to (1) estimate nest survival and nest-site selection in relation to vegetation characteristics and grazing treatment, (2) assess brood survival and brood habitat selection in relation to vegetation characteristics and grazing treatment, and (3) assess the vegetation response to grazing treatments. When I initiated this study, there had been no grazing on the area for the last ~20 years and the vegetation was tall and dense. Tall and dense vegetation may provide suitable nesting habitat (Taylor et al. 1999, Rader et al. 2007), but is not consistent with known brood-rearing habitat preferences for areas with abundant forbs and bare ground (Taylor et al. 1999). Therefore, I predicted that brood-rearing habitat was limiting and thus, bobwhites would select grazed plots for brood-rearing but not for nesting, and that grazing would positively influence brood survival but not nest survival. Furthermore, I predicted that vegetation in grazed plots would be substantially different (shorter, less dense, less percent cover of vegetation) than control plots immediately after grazing but that over the course of the growing season the vegetation would become more similar.

## METHODS

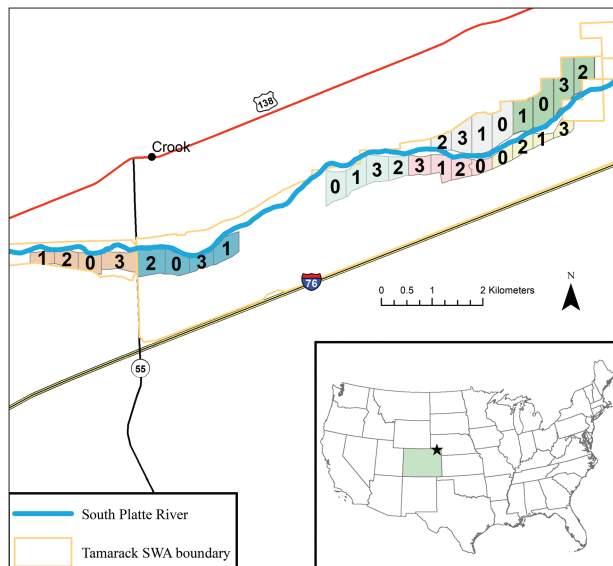
### Study Area

I conducted this study in northeastern Colorado, USA at Tamarack State Wildlife Area (hereafter, Tamarack; 40.8385°N, -102.8053°W) in Logan County from February to September, 2016–2019. Tamarack encompasses 4,775 ha along a 20-km stretch of the South Platte River and is composed of river-bottom riparian forest near the river and grassland/sandhill habitat further away from the river. Bobwhites were generally restricted to the river-bottom riparian area, which consists primarily of plains cottonwood trees (*Populus deltoides*) with understory of sandbar willow (*Salix exigua*), common reed (*Phragmites australis*), and western snowberry (*Symphoricarpos occidentalis*), intermixed with areas of grasses and forbs including western wheatgrass (*Pascopyrum smithii*), downy brome (*Bromus tectorum*), smooth brome (*Bromus inermis*), Japanese brome (*Bromus japonicas*), common ragweed (*Ambrosia artemisiifolia*), thistle (*Cirsium* spp.), and mare's tail (*Erigeron canadensis*).

The elevation of the study area averaged 1,135 m. Historical mean annual precipitation was 42 cm; and during my study annual precipitation was 39, 39, 47, and 48 cm in 2016, 2017, 2018, and 2019, respectively. Daily maximum temperature from April through September averaged 28°C and daily minimum temperature averaged 9°C (Colorado Climate Center, <https://climate.colostate.edu/general.html>). Public hunting is permitted on Tamarack during various small and large game seasons from September to May and the area is divided into 0.4 km (~32 ha each) hunting units along the river, which were used in this study as the experimental units.

### Experimental Design

To evaluate the effects of grazing, I used a randomized block design in which individual plots were grazed within each block. I refer to the hunting units on Tamarack as "plots" and grouped 4 together into each of 7 "blocks" (Figure 1). Within each block, I randomly assigned each plot to be grazed during year 1 (2017), 2 (2018), 3 (2019), or serve as an ungrazed control. Control plots remained the same throughout the study and each grazed plot was only grazed during the 1 year it was randomly selected for treatment. I worked with managers to establish and maintain one or more beef cattle herds in spring of 2017–2019. Cattle in this experiment were used specifically as a tool to manage vegetation with the goal of improving bobwhite habitat, not as a system for beef production. In 2017 and 2018, I used 660 and 630 cattle, respectively, and left them in a plot between 3 and 10 days, depending on the size of the plot, from February 7 to April 10. In 2019, I used 200 cattle and ran them through each grazed plot for 3–15 days from



**FIGURE 1.** Study area map for Tamarack State Wildlife Area in northeastern Colorado where I studied Northern Bobwhite breeding ecology in relation to grazing during 2016–2019. Grazing treatment plots are the numbered polygons (1–3) and blocks are the groups of similarly colored plots ( $n = 7$  blocks). Plot numbers represent the year of the study that the plot was grazed and zeros indicate control plots.

March 18 through April 15 and then again for 4–17 days from April 9 through June 14. Plots varied in size (6–42 ha) resulting in variable cattle densities that ranged from 4.9 to 106 cattle  $\text{ha}^{-1}$  (0.2–0.01  $\text{ha}^{-1}$  cattle $^{-1}$ ). Cattle were 1–2 years old (animal unit [AU] equivalent = 0.7, U.S. Department of Agriculture [USDA] 2003), which equates to stocking rates of 0.29–0.01  $\text{ha}^{-1}$  AU $^{-1}$ . I acknowledge there was undesired variability in grazing intensity among plots and years, but attempted to account for this by using a grazing intensity metric ( $[\text{number of cattle} \times \text{days grazed}] / \text{area of plot}$ ) in analyses. Logistical constraints limited how many cattle I had access to each year and the size of grazing plots. I tried to achieve a similar grazing effect among the plots and years by balancing the size of the plot and the size of the herd with the duration cattle were in plots. I quantified forage utilization in grazed plots in 2019 using the Landscape Appearance Method outlined in Interagency Technical Reference (1999). This method uses visual estimates at a series of points where forage utilization is categorized based on 7 classes describing the degree of utilization: 0–5%, 6–20%, 21–40%, 41–60%, 61–80%, 81–94%, and 95–100%. Based on at least 20 random observations taken in the field in each grazed plot within 1 week after grazing ended, mean forage utilization was 63% (range: 39–85).

Vegetation at Tamarack was dense when I initiated the study, with a large component of exotic cool-season grasses, which are not known to represent quality bobwhite

habitat. The goal of the grazing treatments was to improve or create foraging and brood-rearing habitat by reducing overall vegetation density, creating more bare ground, reducing exotic cool-season grass coverage, and increasing forb coverage. Spring grazing has been reported to reduce the cover of cool-season grasses and facilitate the expansion of warm-season bunchgrass and forbs (Valentine and Stevens 1994). I did not test a full growing-season grazing treatment because I did not want to risk nest trampling or abandonment (Sharps et al. 2017).

## Field Methods

**Bobwhite capture.** From February through early May, I captured bobwhites using baited walk-in traps (Smith et al. 1981). I placed traps throughout Tamarack to attempt to capture a spatially representative sample and checked traps twice daily (mid-morning and at sunset). I used cloth mesh material (Hex mesh, Joanne Fabric) for the trap top to reduce injury to captured quail (Stoddard 1931, Snyder 1978, Wiley et al. 2012) and scraped away litter underneath traps and covered traps with woody and herbaceous debris (Behney et al. 2020). All captured bobwhites were weighed and received a numbered, aluminum leg band (National Band & Tag Company, Newport, Kentucky, USA). On all females and some males, I affixed a  $\leq 6.5$  g necklace-style VHF radio transmitter (Burger et al. 1995, DeMaso et al. 1997, 3.8% of average female mass [170 g], Nelson and Martin 1953). I did not deploy transmitters on bobwhites weighing less than 130 g because it would result in the transmitter weighing  $>5\%$  of female mass. Terhune et al. (2007) concluded that 6-g necklace-style transmitters affixed on bobwhites weighing  $\geq 132$  g had no effect on survival.

**Nest and brood monitoring.** I monitored bobwhite nests and broods in summers of 2016–2019. I located each radio-tagged bobwhite  $\geq 3$  times a week using a homing technique (White and Garrott 1990). Observers walked toward the bird and when they approached it, they circled it at  $\sim 30$  m to pinpoint the bird's location. Personnel estimated the location based on the compass bearing and distance to the bird using a rangefinder from the observer's location. Every attempt was made to avoid flushing birds. Nest sites were determined by observing bobwhites in the same location on multiple, subsequent days. I continued to locate birds  $\geq 3$  times a week and when a bird was off its nest, I went to the nest location, checked its status, counted eggs, and recorded an exact location with a handheld global positioning system. If no opportunities were available to visit the nest while the incubating bird was absent, I flushed the bird during the last week of incubation to get an exact location and count eggs. I continued to monitor nests until success or failure. Observers approached nest sites circuitously from different routes each

visit to avoid creating a path for predators to follow directly to the nest site. For bobwhites with a brood, I used homing to estimate a location  $\geq 3$  times a week without flushing the birds. I flushed the brood at 14-day post-hatch and weekly thereafter (DeMaso et al. 1997) to count chicks to estimate brood survival to 30 days. I considered broods to be active if  $\geq 1$  chick was present, and classified broods as successful if  $\geq 1$  chick survived to 30 days. When no brood was observed, I always proceeded with the next weekly brood flush to confirm brood loss. Estimating survival of young from flush counts can lead to biased results (Orange et al. 2016); however, because I estimated overall brood survival rather than individual chick survival and repeated counts after no chicks were detected, bias should be minimal in this study.

**Vegetation sampling.** I sampled vegetation at nest sites (2016–2019), brood flush sites (2017–2019), and random points associated with each type of used location. Within 3 days of nest completion, or of anticipated nest completion for depredated nests (Gibson et al. 2016a, McConnell et al. 2017), I sampled vegetation at nest sites and 4 associated random sites  $< 200$  m away (i.e., within the distance bobwhites typically move in a day; Liu et al. 2002). Similarly, I sampled vegetation at each brood flush site and 4 associated random points  $< 100$  m away (i.e., within the distance broods typically move in a day; Taylor and Guthery 1994). At each nest, brood site, or random point, I recorded the percent coverage of bare ground, litter, and each species of vegetation within a 1-m<sup>2</sup> sampling frame. I also recorded the lowest 5-cm section visible on a 2.5-cm diameter pole, read from 4 m in 4 directions, 90° apart, from 1 m above the ground (Robel et al. 1970).

To quantify the effects of grazing on vegetation, I sampled vegetation using the same measurements described above, at 5 random points within each grazed or control plot, in spring (directly after grazing; April–May), mid-summer (June–July), and late summer (August–September), 2017–2019. I chose these dates to compare initial, pre-growing season effects of grazing with those toward the middle and end of the growing season to determine the duration of grazing effects on vegetation. These points were not associated with bird locations but were meant to represent general vegetation characteristics within each grazed or control plot.

### Statistical Analyses

I used hierarchical models in a Bayesian framework for all analyses. I fit models using JAGS 4.3.0 (Plummer 2017) through the *rjags* package (Plummer 2019) in R (R Core Team 2020). I used vague priors. For models with a logit link function, I assigned coefficients normal (mean = 0, SD = 1.4) priors to approximate a uniform (min = 0, max = 1) prior on the probability scale (Northrup and Gerber 2018). For coefficients in models without a logit

link function, I used normal (0, 100) priors. I assigned standard deviations uniform (0, 10) prior distributions. I fit 3 chains for at least 35,000 iterations following 10,000 iterations for burn-in. I assessed convergence by visually examining trace plots as well as with Gelman and Rubin's convergence diagnostic in the R package *CODA* (Plummer et al. 2006) to ensure it was close to one for all parameters.

**Nest and brood survival.** I used the hierarchical model described by Schmidt et al. (2010) to estimate daily survival probabilities and assess factors that influence survival of nests and broods. I considered nests and broods successful if at least 1 egg hatched or 1 chick survived to 30 days. I modeled whether nest or brood  $i$  was observed alive ( $y = 1$ ) or dead ( $y = 0$ ) on day  $t$  as a series of Bernoulli trials where  $\phi_{it}$  is the probability of individual  $i$  being alive at time  $t$  given it was alive at time  $t - 1$ . The model took the form:

$$y_{it} \sim \begin{cases} 0 & \text{for } y_{it-1} = 0 \\ \text{Bernoulli}(\phi_{it}) & \text{for } y_{it-1} = 1 \end{cases} \quad (1)$$

$$\phi_{it} = \text{logit}^{-1}(a_0 + a_{q[i]} + B_1 X_{it} + B_2 X_i)$$

where  $a_0$  was the intercept,  $a_{q[i]}$  was a random effect to account for multiple nests or brood observations from the same bird  $q$  ( $Q = 79$ ),  $B_1 X_{it}$  was a vector of coefficients and time-varying covariates (date and nest age), and  $B_2 X_i$  was a vector of coefficients and covariates that vary among nests or broods (grazing treatment, year, sex of incubating adult, vegetation characteristics). I standardized all continuous covariates by subtracting the mean and dividing by the standard deviation so that their coefficient values would be directly comparable estimates of effect sizes. I calculated period survival (nest success = 23 days, brood success = 30 days) as a derived parameter in the model which also estimates variability associated with period survival.

To assess the importance of predictor variables, I used a multi-stage modeling strategy. Each stage contained different amounts of multicollinearity so I used different model/variable selection techniques for different stages. For nest survival, I first found the most supported form of the grazing effect. I tested 6 forms of the grazing effect: grazing treatment with 4 levels (grazed current year, grazed 1 year ago, grazed 2 years ago, ungrazed), 3 levels (grazed current year, grazed any previous year, ungrazed), 2 levels (grazed current year, not grazed current year), and the grazing intensity metric ([cattle  $\times$  days] ha<sup>-1</sup>, a continuous variable) interacting with each form of the grazing treatment variable. The different forms of the grazing effect were essentially representing the same thing, so to avoid collinearity, I did not include multiple forms of the grazing variables in the same model. I fit 7 models including a null model and 6 others, each including a different form of the

grazing effect. I only included the grazing intensity metric in interactive relationships with the grazed factor variables to allow the grazing intensity effect to be different between plots that were grazed and those that may not have been grazed yet in the study. I compared these models using Deviance Information Criteria (DIC). I then used the most supported form of the grazing variable (or null model if it was best) in a model also including date, nest age, and sex of the incubating bird. These variables were not correlated, so I included them in an additive relationship in the same model and advanced variables to the final modeling stage based on whether their coefficient's 90% credible interval excluded 0. I did not include any vegetation variables up to this point because if grazing treatment had an effect on survival, it would most likely be because of effects on vegetation, and therefore, grazing treatment would be confounded with the vegetation variables.

In the final stage of modeling, I included the vegetation characteristics as well as any variables other than grazing treatment that were important in previous modeling stages. The vegetation variables included percent litter, warm-season grass, total grass, bare ground, forb, and woody vegetation, as well as the height of the tallest vegetation in the sample frame and the visual obstruction reading. Percent cool-season grass was correlated with percent total grass ( $r = 0.88$ ) so I only used percent total grass for modeling. Other vegetation variables were not correlated ( $r < 0.5$ ) so I included all these vegetation variables in a single model and present posterior means and 90% credible intervals for each variable's coefficient. I also fit a second model with vegetation variables as quadratic effects. I considered variables important predictors of nest survival if their coefficient's credible interval excluded 0.

For brood survival, I fit similar models as described for nest survival. Because broods moved among plots, I used the percentage of brood locations in grazed plots to test for grazing effects. Similar to nest survival, I tested different forms of the grazing treatment variable: percentage of locations in plots grazed that year, grazed that year or the previous year, or grazed any year. I compared these grazing treatment models and a null model using DIC. To the most supported model from stage 1, I added date and brood age in a single model and considered them important variables if their coefficient's 90% credible interval excluded 0.

I assessed model fit using posterior predictive checks with Bayesian  $P$ -values as described in Schmidt et al. (2010). The Bayesian  $P$ -value was the percentage of iterations for which the observed data fit metric described in Schmidt et al. (2010) exceeded that of data simulated from the fitted model, where extreme values near 0 or 1 indicate poor fit.

**Nest and brood site selection.** I assessed nest and brood site selection at 2 spatial scales. Each point was labeled 1 if it was chosen as a nest or brood location and 0 if it was a random point representing available habitat. I modeled this binary variable as a Bernoulli distributed response variable as a function of vegetation and grazing treatment covariates. Available points were conditional on specific used locations, so I included a nest or brood point identifier as a random effect to group the available points with the nest or brood point from which they were generated (Gillies et al. 2006).

For the fine-scale analysis of nest and brood site selection, I used the 4 random points surrounding nest ( $\leq 200$  m) and brood ( $\leq 100$  m) used locations at which vegetation samples were taken to represent available habitat. I first found the most supported form of the grazing variable using the same methods outlined for the survival analysis with the 7 models including a null model and 6 others each representing a different form of the grazing effect (see survival section above for description of models). I was also interested in vegetation characteristics' effect on habitat selection, so in a second stage, I included all vegetation variables in a single model and considered variables important in predicting site selection if their coefficient's 90% credible interval excluded 0. I also tested for quadratic effects of vegetation variables by including all variables as quadratic effects together in a model. I concluded that a quadratic effect of a vegetation variable was an important predictor of habitat selection if the coefficient's 90% credible interval excluded 0. I did not use model selection in this second stage because other than percent cool-season grass and percent total grass ( $r = 0.92$ ), variables were not correlated ( $r < 0.5$ ) so I could include them all in the same model. I did not use percent cool-season grass in modeling to avoid collinearity.

For the larger-scale analysis of nest and brood site selection, I buffered locations leading up to the nest or brood flush location (Arthur et al. 1996, Johnson et al. 2006, Dyson et al. 2018). For nests, I buffered each location from 1 April through nest initiation by the distance moved to get to the location and then merged those buffers together to represent available habitat associated with each nest. Specifically, I buffered used location  $t$  by the distance moved from location  $t - 1$  to  $t$ . I generated 20 random points within each nest's available habitat and classified each point based on whether they were in plots grazed that year, grazed previous year, grazed 2 years prior, or ungrazed. For brood locations, I used a similar method in which I buffered each point from hatch to the brood flush event by the distance moved to get to each location. I generated 20 random points within these buffers and classified them regarding grazing treatment. For this larger-scale brood and nest-site selection analysis, I used the same models described above

for the fine-scale site selection analysis but because I did not sample vegetation in the field at this larger scale, I only used grazing treatment and grazing intensity as predictors in addition to year. I fit the same 7 models outlined in the survival analysis including a null model and 6 others, each including a form of the grazing effect. I compared models using DIC and assessed overall model fit using deviance as the test statistic (Smith et al. 2018) with Bayesian  $P$ -values.

For both the fine-scale and larger-scale habitat selection analyses, I assessed the sensitivity of the model parameters to the number of available points generated per nest or brood by running the model with 1 through 20 available points per location for the larger-scale analysis and 1 through 4 available points per location for the fine-scale analysis. I visually examined plots of parameter values vs. the number of available points to assess whether the curves had stabilized regarding the number of available points.

**Vegetation response to grazing.** I modeled maximum vegetation height, visual obstruction, percent bare ground, percent forbs, percent warm-season grasses, percent cool-season grasses, and percent woody vegetation separately using similar models but with different distributions (described below) that were appropriate for each data type. I included point nested within plot and plot nested within block as random effects in all models to account for the lack of independence of repeated measurements at the same point within plots, within blocks. I represented the nested structure by including the effect of block  $j$  as the prior mean for plot  $k$  within block  $j$  and I included the effect of plot  $k$  as the prior mean for the effect of point  $l$  within plot  $k$ :

$$a_j \sim \text{normal} (0, \sigma^{\text{block}}) \quad (2)$$

$$a_k \sim \text{normal} (a_{j[k]}, \sigma^{\text{plot}})$$

$$a_l \sim \text{normal} (a_{k[l]}, \sigma^{\text{point}})$$

I included year, sampling occasion, and treatment as fixed effects. To represent my prediction that grazed plots would be substantially different than control plots immediately after grazing but over the course of the growing season becomes more similar, I included an interaction between sampling occasion and grazing treatment or grazing intensity. If the grazing effect did not change through the growing season, a model including an additive relationship between occasion and treatment should outperform the interaction model. I also fit a null model, and models only including treatment or occasion. I compared models using DIC and assessing whether 90% credible intervals for coefficients overlapped 0. For each model including a treatment effect, I fit models including treatment with

4 levels (grazed that year, grazed previous year, grazed 2 years ago, control), 3 levels (grazed that year, grazed any previous year, control), and 2 levels (grazed that year, not grazed that year). For each vegetation data type, I present the model structure below.

Maximum vegetation height was a positive-only variable, therefore I used a lognormal distribution:

$$\log (y^{\text{height}}_i) \sim \text{normal} (\mu_i, \sigma^{\text{height}}) \quad (3)$$

$$\mu_i = a_0 + a_{l[i]} + BX_i$$

where  $y^{\text{height}}_i$  is observation  $i$  of vegetation height,  $\sigma^{\text{height}}$  is the model standard deviation,  $a_0$  is the overall intercept,  $a_{l[i]}$  is the nested random effect for point  $l$  for observation  $i$  as shown in Equation (2), and  $BX_i$  is a vector of coefficients and covariates listed above.

I used a binomial distribution for visual obstruction because a specific numbered band on the pole was observed out of the total number of bands on the pole (30):

$$y^{\text{vis}}_i \sim \text{binomial} (p_i, 30) \quad (4)$$

$$p_i = \text{logit}^{-1} (a_0 + a_{l[i]} + BX_i)$$

where  $y^{\text{vis}}_i$  is observation  $i$  of visual obstruction,  $a_0$  is the overall intercept,  $a_{l[i]}$  is the nested random effect for point  $l$  for observation  $i$  as shown in Equation (2), and  $BX_i$  is a vector of coefficients and covariates listed above.

For percent cover variables (bare ground, forb, warm-season grass, cool-season grass, total grass, litter), I used zero-and-one-inflated beta models (Ospina and Ferrari 2010). The beta distribution provides support for values between 0 and 1. Including 0 and 1 inflation allowed me to include all data, including zeros and ones, without truncating or replacing any values (i.e., replacing 0 with 0.01). The model has 3 parts: a Bernoulli model for discrete values (0 or 1,  $y^{\text{disc}}$ ), a beta model for continuous values (between 0 and 1,  $y^{\text{cont}}$ ), and a Bernoulli model for the mixing parameter ( $\epsilon$ ), which is the probability that any observation ( $y^{\text{indicate}}$ ) is discrete rather than continuous. The data were specified separately into the model for each of the 3 submodels. I refer to the 0 and 1 data as  $y^{\text{disc}}$ , the data between 0 and 1 as  $y^{\text{cont}}$ , and the data noting which observations were discrete vs. continuous as  $y^{\text{indicate}}$ , with subscripts  $j$ ,  $k$ , and  $i$  representing observations within the 3 datasets, respectively. The overall model took the form: for  $y^{\text{disc}}$  (0 or 1):

$$y^{\text{disc}}_j \sim \epsilon \times \text{Bernoulli} (p_j) \quad (5)$$

$$p_j = \text{logit}^{-1} (a_0 + a_{l[j]} + BX_j)$$

for  $y^{\text{cont}}$  (between 0 and 1):



**TABLE 1.** Summary of model selection results for grazing variables in the nest survival, fine- and large-scale nest, and brood site selection analyses for Northern Bobwhites in northeastern Colorado, 2016–2019. Values indicate the rank of models and values in parentheses show  $\Delta$ DIC for each analysis. Graze2 is grazing treatment with 2 levels: grazed current year, not grazed current year. Graze3 is grazing treatment with 3 levels: grazed current year, grazed any previous year, ungrazed. Graze4 is grazing treatment with 4 levels: grazed current year, grazed 1 previous year, grazed 2 years ago, ungrazed. Int. is the grazing intensity metric: (number of cattle  $\times$  days present)/plot area. Full model selection results are shown in [Supplementary Material Tables S1, S2, S4, S5, and S7](#).

Model	Nest survival	Nest selection: fine scale	Nest selection: large scale	Brood selection: fine scale	Brood selection: large scale
Null	1 (0)	1 (0)	7 (4.1)	1 (0)	1 (0)
Graze3	2 (0.7)	3 (2.3)	4 (2)	3 (3.2)	3 (1.7)
Graze2	3 (2.5)	2 (1.4)	1 (0)	2 (1.8)	2 (1.6)
Int $\times$ graze2	4 (2.6)	5 (5.4)	2 (1.4)	5 (4.8)	7 (5.4)
Graze4	5 (3.9)	4 (3.5)	5 (2.9)	4 (4.2)	5 (2.9)
Int $\times$ graze4	6 (4.1)	7 (8.7)	3 (1.5)	7 (9.0)	6 (4.4)
Int $\times$ graze3	7 (8.1)	6 (7.6)	6 (3.5)	6 (7.9)	4 (2.6)

$$y_k^{\text{cont}} \sim (1 - \varepsilon) \times \text{beta}(\mu_k \times \Phi, (1 - \mu_k) \times \Phi) \quad (6)$$

$$\mu_k = \text{logit}^{-1}(a_0 + a_{l[k]} + BX_j)$$

where the 2 parameters of the beta distribution were defined by  $\mu$  and  $\Phi$  (Figueroa-Zuniga et al. 2013), and  $\Phi$  was a constant precision parameter,  $a_0$  was the overall intercept,  $a_l$  was the nested random effect for sample point  $l$  as shown in Equation (2), and  $BX$  was a vector of coefficients and covariates listed above. I held parameters constant between the discrete and continuous components of the model but used different values for the mixing parameter submodel:

for  $y^{\text{indicate}}$  (whether a value was discrete or continuous):

$$y_i^{\text{indicate}} \sim \text{Bernoulli}(\varepsilon_i) \quad (7)$$

$$\varepsilon_i = \text{logit}^{-1}(c_0 + c_{l[i]} + TX_i)$$

where  $c_0$  was the overall intercept,  $c_l$  was the nested random effect for sample point  $l$  as shown in Equation (2), and  $TX$  was a vector of coefficients and covariates listed above.

## RESULTS

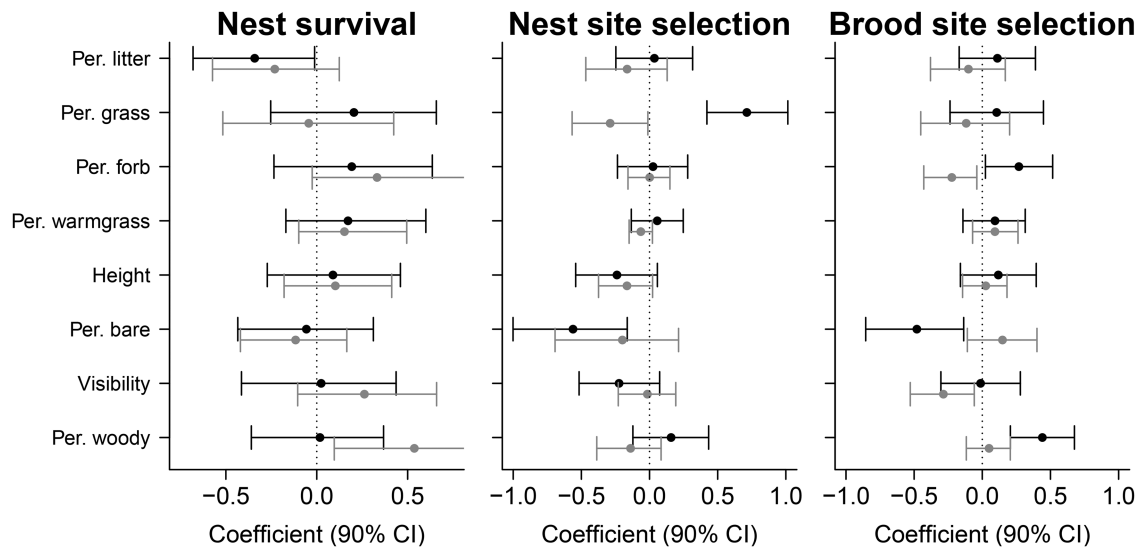
### Nest Survival

I included 91 nests (74 female- and 17 male-incubated) in the nest survival analysis. I excluded 7 additional nests from analysis due to research-caused abandonment (researchers inadvertently flushed birds during laying or early incubation). All models converged (Gelman–Rubin values  $< 1.05$ ) and posterior predictive checks indicated adequate model fit (Bayesian  $P$ -values = 0.5–0.7). In the first stage of modeling, which included grazing treatment variables, the null model had the lowest DIC (Table 1, Supplementary Material Table S1). Although the model including grazing treatment with 3 levels appeared competitive ( $\Delta$ DIC = 0.7), credible intervals around derived

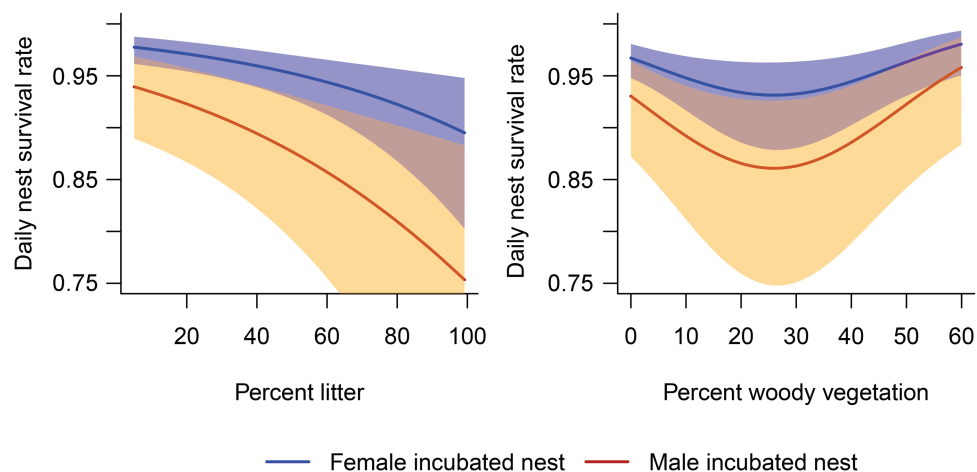
parameters calculating the difference between daily survival rate among the 3 grazing treatment levels overlapped 0 (control – grazed previous = med: 0.03, 90% CI: –0.02 to 0.16; control – grazed same year = 0.02, 90% CI: –0.03 to 0.16; grazed previous – grazed same year = –0.01, 90% CI: –0.13 to 0.12). Therefore, I did not consider a grazing treatment variable in any subsequent nest survival models. In the next modeling stage, the only model to outperform the null model included sex ( $B_{\text{male}} = -0.92$ , 90% CI: –1.6 to –0.3; Table 2). In the final stage of modeling, based on whether coefficient credible intervals contained 0, percent litter in a linear form, percent woody vegetation in a quadratic form (Figure 2), and sex were the only important variables. Nests with more litter around the nest, those with moderate amounts of woody vegetation, and male-incubated nests exhibited lower survival rates (Figure 3). Mean daily survival rate for female-incubated nests, while holding percent litter and woody vegetation constant at their mean, was 0.96 (90% CI: 0.95–0.97) and for males was 0.90 (90% CI: 0.82–0.94). Overall model-predicted 23-day nest success for female-incubated nests was 0.39 (90% CI:

**TABLE 2.** Model selection table for stage 2 of the survival analysis evaluating the effects of sex of incubating adult, date, and nest age on daily survival rate of Northern Bobwhite nests in northeastern Colorado, 2016–2019.  $k$  is the number of parameters that were estimated in the model and  $\Delta$ DIC is the difference in Deviance Information Criteria between each model and the best model (lowest DIC).

Model	$k$	$\Delta$ DIC
Sex	6	0.0
Null	5	0.7
Date	6	1.8
Date + sex	7	2.1
Age + sex $\times$ date	9	6.9
Age + date	7	10.4
Age	6	13.3
Age + sex	7	15.1
Age + date + sex	8	18.9
Age $\times$ sex + date	9	22.8



**FIGURE 2.** Northern Bobwhite nest survival, nest site selection, and brood site selection coefficients  $\pm$  90% CI for vegetation characteristics. Gray points and bars represent quadratic effect coefficients and black points and bars represent linear effect coefficients. I monitored nests and broods in northeastern Colorado during 2016–2019.



**FIGURE 3.** Predicted daily survival rate for male (orange) and female (blue) incubated Northern Bobwhite nests as a function of percent litter and woody vegetation within 1 m of the nest in northeastern Colorado, 2016–2019. Shaded areas represent 90% credible intervals.

0.28–0.52) and for male-incubated nests was 0.08 (90% CI: 0.01–0.26).

### Nest Site Selection

I included 94 nests, each with 4 associated random points, in the nest site selection analysis. All models converged (Gelman–Rubin values  $<1.05$ ) and posterior predictive checks indicated adequate model fit (Bayesian  $P$ -values = 0.6–0.7). Coefficients appeared to be insensitive to the number of available random points per nest at 4 random points for the fine-scale analysis and 20 random points per nest for the larger-scale analysis (Supplementary Material Figure S1). For the fine-scale

analysis, none of the grazing treatment variables outperformed the null model (Table 1, Supplementary Material Table S2). Credible intervals for vegetation variable coefficients that did not overlap 0 included a quadratic effect of percent grass and linear effect of percent bare ground (Figure 2). Relative probability of use was positively related to percent grass and negatively related to percent bare ground (Figure 4, Supplementary Material Table S3).

For the larger-scale analysis, the top model included grazing treatment with 2 levels: grazed that year and not grazed that year (ungrazed and plots grazed during previous years; Table 1, Supplementary Material Table S4).

**TABLE 3.** Model selection table for stage 1 of the survival analysis assessing the effect of grazing treatment on brood survival in northeastern Colorado, 2017–2019. Grazing treatment variables were the percentage of time spent in plots grazed the same year (Graze same), grazed the previous year (Graze prev. 1), grazed the same year, previous year, or 2 years prior (Graze within 2), and grazed the same year or the previous year (Graze within 1).  $k$  is the number of parameters that were estimated in the model and  $\Delta$ DIC is the difference in Deviance Information Criteria between each model and the best model (lowest DIC).

Model	$k$	$\Delta$ DIC
Null	4	0.0
Graze same	5	1.6
Graze prev. 1	5	1.6
Graze within 2	5	2.3
Graze within 1	5	2.7

Models including the continuous grazing intensity metric were competitive based on DIC, but because they estimated more parameters and still underperformed the simpler model, I based inference on the top model alone. Relative probability of use was greater in plots not grazed in the current year (mean = 0.05, 90% CI: 0.04–0.07) than in plots that were grazed in the current year (0.02, 90% CI: 0.01–0.04).

### Brood Survival

I included 41 broods in the brood survival analysis and 19 survived to 30 days. All models converged (Gelman–Rubin values <1.05) and posterior predictive checks indicated adequate model fit (Bayesian  $P$ -values = 0.4–0.5). In the first stage of modeling focused on grazing treatment variables, no form of grazing treatment outperformed the null model (Table 3). In the second stage of modeling, date ( $B_{\text{date}} = 0.04$ , 90% CI: –0.39 to 0.28) and brood age ( $B_{\text{age}} = -0.29$ , 90% CI: –0.69 to 0.12) were poor predictors of brood daily survival rate. Based on the null model (including year), daily survival rate of broods was 0.97 (90% CI: 0.96–0.98) and 30-day brood success was 0.43 (90% CI: 0.32–0.55) pooled across years.

### Brood Site Selection

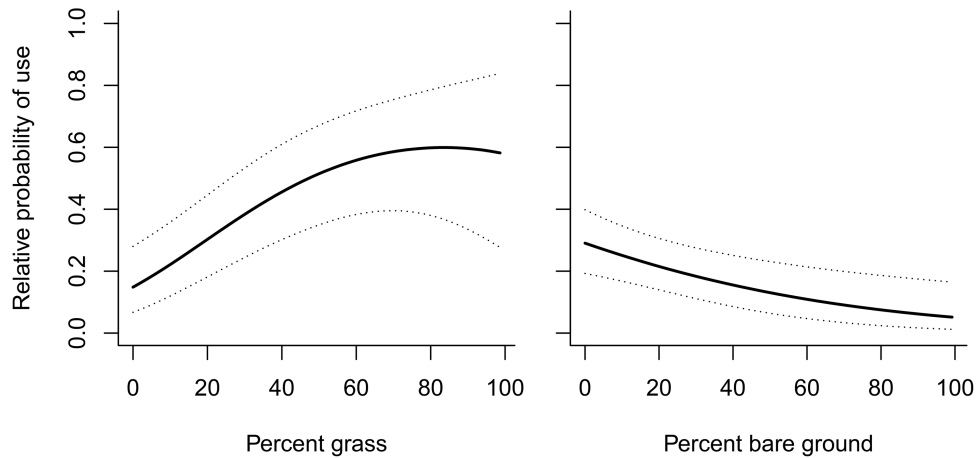
I included 90 brood locations from 35 bobwhites in the brood site selection analysis. All models converged (Gelman–Rubin values <1.05) and posterior predictive checks indicated adequate model fit (Bayesian  $P$ -value = 0.6). Coefficients appeared to be insensitive to the number of available random points per brood location at 4 random points for the fine-scale analysis and 20 random points per brood location for the larger-scale analysis (Supplementary Material Figure S2). For the fine-scale analysis, no forms of the grazing treatment variable were more parsimonious than the null model (Table 1, Supplementary Material Table S5). Credible intervals for

vegetation variable coefficients that did not overlap 0 included linear effects of percent woody vegetation and percent bare ground, and quadratic effects of percent forbs and visual obstruction (Figure 2). Relative probability of use was positively related to percent woody vegetation and negatively related to percent bare ground (Figure 5, Supplementary Material Table S6). Relative probability of use increased with increasing percent forbs to ~20% and then declined with further increases in forb coverage (Figure 5). In relation to visual obstruction, use was greatest at low and high visual obstruction (Figure 5). In the larger-scale brood site selection analysis, no form of the grazing treatment variable outperformed the null model (Table 1, Supplementary Material Table S7).

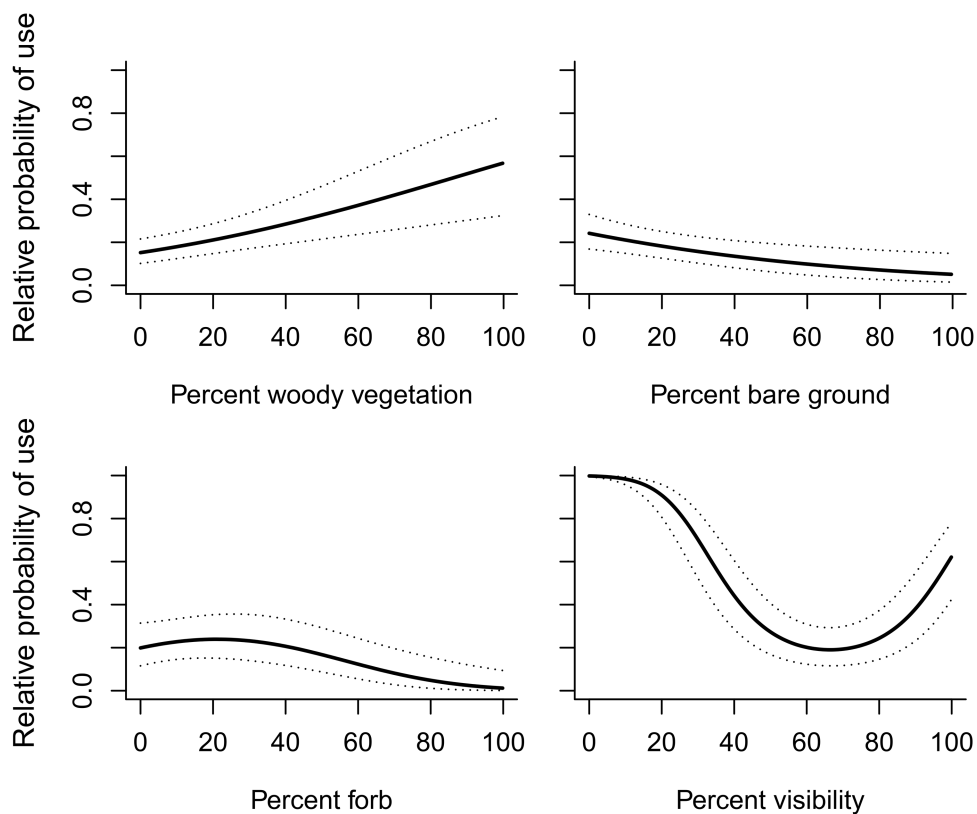
### Vegetation Response to Grazing

I conducted 855 vegetation samples. All models converged (Gelman–Rubin values <1.05) and posterior predictive checks indicated adequate model fit (Bayesian  $P$ -values = 0.4–0.6). Models including an interaction between sampling occasion and grazing treatment were the most supported based on DIC for all vegetation characteristics except warm-season grasses and woody vegetation (Supplementary Material Table S8). For tallest vegetation and percent forbs, the most supported model included grazing treatment with 2 levels (grazed that year, not grazed that year) interacting with sampling occasion. For percent bare ground, cool-season grass, total grass, and litter the best model included grazing treatment with 3 levels (grazed that year, grazed any previous year, ungrazed control) interacting with sampling occasion. Visual obstruction was best described by a model including grazing treatment with all 4 levels (grazed that year, grazed last year, grazed 2 years ago, ungrazed control) interacting with sampling occasion. For warm-season grasses, the most supported model included grazing treatment with 2 levels in an additive relationship with sampling occasion. For woody vegetation, the most supported model included only sampling occasion, but a competitive model also included treatment with 4 levels in an additive relationship. A third competitive model included occasion interacting with grazing intensity. However, because the simpler model only including occasion had a lower DIC and there was little difference in predicted values among grazing treatments or intensities, I based inference for woody vegetation on the model only including occasion. Overall, there was little model selection uncertainty. The second-best model was at least around 2 DIC units behind the top model for every vegetation characteristic except woody vegetation.

Most vegetation showed effects directly after grazing but those effects tended to disappear or weaken throughout the growing season (Figure 6). However, percent forb cover



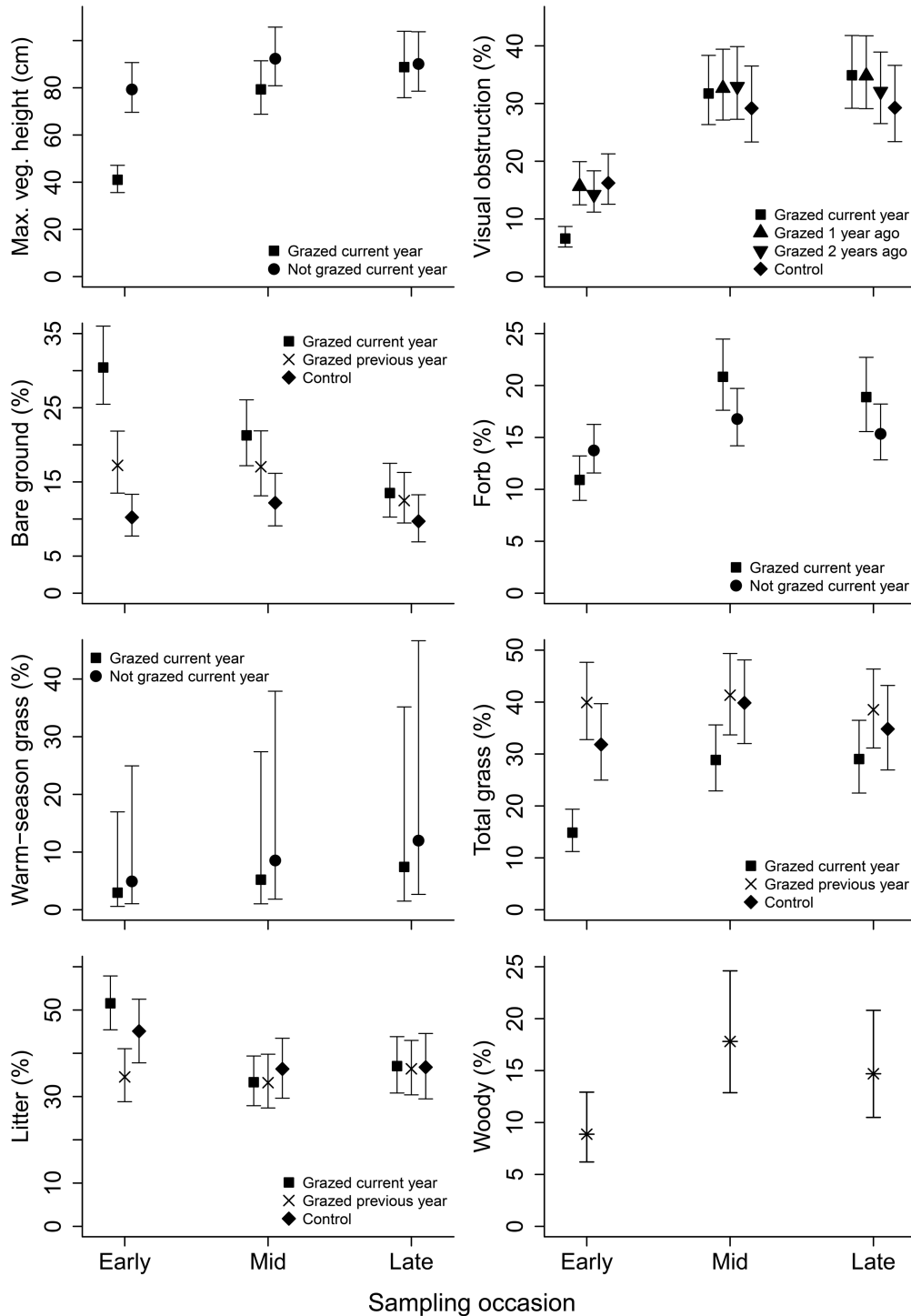
**FIGURE 4.** Predicted relative probability of use for Northern Bobwhite nest sites as a function of percent grass and percent bare ground in northeastern Colorado, 2016–2019. Dotted lines represent 90% credible intervals.



**FIGURE 5.** Predicted relative probability of use for Northern Bobwhite brood sites as a function of percent woody vegetation, percent bare ground, percent forb coverage, and percent visibility in northeastern Colorado, 2017–2019. Visibility was estimated from a Robel pole and was the inverse of visual obstruction. Dotted lines represent 90% credible intervals.

tended to be greater in grazed plots during mid- and late-summer sampling occasions even though directly after grazing in the spring, forb cover was less in grazed plots than ungrazed plots (Figure 6). There tended to be less total grass throughout the growing season in plots grazed that year compared with ungrazed control plots and plots

grazed in previous years (Figure 6). Cool-season grass followed the same pattern as total grass ( $r = 0.7$ ), so I only show total grass in Figure 6. There was substantial variability in my estimates of warm-season grass cover, which also had the lowest number of detections (13% of samples vs. 63% for cool-season grass).



**FIGURE 6.** Predicted vegetation characteristics from the most-supported model for each vegetation characteristic sampled at random points throughout grazed and control plots during early (April), mid (June–July), and late (August–September) sampling occasions in northeastern Colorado, 2017–2019. The most-supported model varied among vegetation class which is why the legends are different among the panels. Error bars represent 90% credible intervals.

**DISCUSSION**

High-intensity short-duration grazing during spring had no detectable positive benefits on the reproductive ecology

of bobwhites in this study. I detected effects of vegetation on nest survival and nest and brood site selection; however, grazing treatment variables were poor predictors of habitat selection or nest survival. Grazing had substantial effects

on vegetation immediately after grazing (beginning of bobwhite nesting season); however, many of these vegetation effects diminished throughout the growing season. The effects of grazing on vegetation during early to mid-summer were consistent with bobwhite brood habitat preferences, but by late summer when broods were present these vegetation effects were weak to nonexistent. Based on these results, high-intensity short-duration grazing during spring appears to be an ineffective strategy to improve bobwhite breeding habitat in Colorado. Many different types of grazing strategies exist and generalizations beyond the specific grazing regime I tested should be avoided.

It was surprising that I did not find a positive response of broods to grazing, given the success of high-intensity short-duration grazing reported in other studies (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992) and the previously reported brood habitat preference for areas with low vegetation density (Taylor et al. 1999). In this study, broods selected areas with moderate amounts of forbs, more woody vegetation, less bare ground, and avoided areas with moderate visibility compared to available habitat. Brood selection for forbs has been previously reported (Taylor et al. 1999), likely as a function of greater food availability (Jamison et al. 2002). However, my finding of selection against bare ground is interesting and counter to previous research (Taylor et al. 1999) and prescriptions for brood habitat management (National Bobwhite Conservation Initiative 2015). Bare ground is necessary to facilitate chick movement and feeding (Doxon and Carroll 2010). The discrepancy in effects of bare ground between this study and other research may be due to bare ground being more abundant in this study (10–15% in ungrazed areas; Figure 6) compared with what was reported in Taylor et al. (1999; 8.4%). I take this finding to indicate that the portions of my study area that I considered available for broods, contained sufficient bare ground. Therefore, my results are not necessarily consistent with the hypothesis that bobwhite populations were being limited by the availability of more open feeding and brood-rearing habitat in my study area. However, in addition to bare ground, high forb cover is thought to be an important component of brood-rearing habitat, and in this study, bobwhites selected areas with moderate amounts of forbs.

Nest site selection at Tamarack was consistent with other research (Taylor et al. 1999, Townsend et al. 2001, Lusk et al. 2006, Rader et al. 2007); bobwhites selected nest sites with more grass and less bare ground. Bobwhites also tended to select nest sites where the vegetation was shorter than available sites; however, this effect was weak and credible intervals around this coefficient overlapped 0. Furthermore, this finding is counter to previous research that has reported selection for taller vegetation (Lusk et al. 2006, Rader et al. 2007). This discrepancy may be a result of mean vegetation height in this study

(80–90 cm in ungrazed areas; Figure 6) being substantially greater than that reported in other literature (64–76 cm: Lusk et al. 2006, 47 cm: Rader et al. 2007). At the larger scale, I found a negative impact of grazing on nest-site selection. This finding was not surprising given the known nest site habitat preferences of bobwhites for taller, denser vegetation (Taylor et al. 1999). The availability of suitable nest sites is not perceived to be a limiting factor for bobwhites at Tamarack because the vegetation is very dense with abundant grasses.

Nest survival was influenced by percent litter and woody vegetation around the nest as well as sex of the incubating adult. Male-incubated nests had lower survival rates than female-incubated nests; however, the sample size for male-incubated nests was substantially less. Previous research (Burger et al. 1995) has not documented this discrepancy in nest survival between sexes, which could have implications for population models that assume constant nest survival across sexes (Sandercock et al. 2008, Williams et al. 2012). In Mountain Plovers (*Charadrius montanus*), Dinsmore et al. (2002) hypothesized that differences in nest survival between sexes would be due to differences in nest initiation dates. In my study, mean nest initiation date was 10 days later for males; however, I did not detect an effect of date on nest survival. As for vegetation, like my results, Taylor et al. (1999) found that litter negatively influenced bobwhite clutch success in Kansas even though litter had a positive effect on nest-site selection. This pattern of selection for litter but with negative effects on nest survival has also been observed in grassland songbirds (Lusk and Koper 2013), although litter has also been reported to exert a positive effect on nest survival (Hughes et al. 1999). Westemeier (1973) suggested that excess litter may alter the nest microclimate as well as suppress new plant growth, which may reduce nest concealment; however, I did not find an effect of visual obstruction on nest survival. Overall, none of the variables that were important in predicting nest site selection were important in nest survival. It is interesting that bobwhites exhibited these nest site selection preferences that were not associated with increased nest survival. One theory is that bobwhites may select nest sites to maximize some factor other than nest survival. For example, Gibson et al. (2016b) found that nest-site selection of Greater Sage-Grouse (*Centrocercus urophasianus*) was better at predicting chick survival than nest survival, which indicates that females selected nest sites based on brood-rearing habitat quality. Alternatively, in my study, there may not have been sufficient variation in selected nest site vegetation to cause detectable effects on nest survival.

Most vegetation categories showed substantial grazing effects during the early sampling period directly after grazing (start of bobwhite nesting), but these effects diminished throughout the season and by the late sampling occasion

(bobwhite brood-rearing period), little difference was evident between grazed and control plots. Similarly, Sedgwick and Knopf (1987, 1991) observed few differences in vegetation and no differences in breeding songbird densities following fall-winter grazing at stocking rates of 0.46 ha AU<sup>-1</sup> in the same study area. Forbs were the exception in this study; grazed plots continued to support greater amounts of forb cover later in the growing season. Forb cover was important in brood habitat selection, and during the late vegetation sampling occasion, a time when many broods were present, the grazed plots tended to contain more forb cover than control plots. Positive response of forbs to grazing has been reported elsewhere (Hammerquist-Wilson and Crawford 1981, Hayes and Holl 2003, Fondell and Ball 2004) and may be a result of increased bare ground and overall decreased vegetation height directly after grazing, which can reduce competition with grasses (Hayes and Holl 2003). One of the reasons I chose to test grazing treatments during spring was to reduce the cover of cool-season grasses (Valentine and Stevens 1994) and facilitate the expansion of warm-season bunchgrasses and forbs. Overall, given the trend of greater forb cover in grazed plots that tended to last through multiple seasons, intensive spring grazing seemed to have a neutral to potentially positive impact on the vegetation, given known bobwhite habitat preferences. However, any effects of grazing on the vegetation were not strong enough to elicit a response that was detectable in the bobwhite habitat selection data.

Previous research on high-intensity short-duration grazing took place in south Texas where the climate is less arid than northeastern Colorado. The greater rainfall typical of south Texas may indicate greater productivity (annual herbaceous biomass production), which can determine the optimal seral stage of bobwhite habitat for an area (Spears et al. 1993). On less productive sites, Spears et al. (1993) predicted that bobwhites prefer later successional communities and therefore, less disturbance than in areas with greater productivity. If my study area was less productive than where the previous research was conducted in south Texas, then the optimal management strategy may be to disturb vegetation less, rather than using intensive grazing treatments. However, based on my vegetation results, the vegetation responded quickly to disturbance and during a single growing season, grew back to the point where there was little to no detectable effect of grazing on vegetation. The high vegetation productivity at Tamarack was likely the result of being in a riparian area, which can support high vegetation productivity in arid regions (Hubbard 1977, Patten 1998).

Additional differences between my study and previous grazing studies were stocking rates and timing of grazing. Stocking rates were generally greater in this study (0.29–0.01 ha AU<sup>-1</sup>) than what has been reported in previous research (stocking rates 0.5–9.5 ha AU<sup>-1</sup>; Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988,

Wilkins and Swank 1992) and the duration of grazing was generally shorter than previous studies. Furthermore, in this study, grazing only occurred during spring, whereas in most previous research, grazing occurred year-round in a rotational system. The previous research likely observed effects of grazing because they grazed throughout the growing season whereas in this study grazing only occurred at the very beginning of the growing season.

Because intensive spring grazing did not provide any detectable benefits to bobwhites, I recommend further study of alternative modes of vegetation management. Historically, natural fire occurred in this prairie grassland every 10–30 years (Paysen et al. 2000), although the frequency and intensity that riparian areas burned are less well known (Dwire and Kauffman 2003). Fire is an important management tool used in other parts of the bobwhite range to reset succession (Rosene 1969, Kamps et al. 2017) and may be worth testing in Colorado. Other options such as chemical application has shown promise elsewhere (Jones and Chamberlain 2004) and should be explored as well. Grazing during other times of year, including during the bobwhite breeding season, may be worthwhile given the lack of any lasting effect on vegetation from spring grazing and the reported positive effects of grazing throughout the year (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992). Rather than cease grazing in late spring, further research could examine the value of continuing to rotate the herd through experimental plots for short durations throughout the entire growing season or even through autumn. Lastly, warm-season grasses made up a small component of overall grass in this study but have been reported to represent an important component of bobwhite habitat elsewhere (Parsons et al. 2000, Richardson et al. 2020). Given the importance of warm-season grasses to bobwhites, the lack of any grazing effect on coverage of warm-season grasses may be a reason that I did not detect an effect of grazing on bobwhite habitat selection. Future research focusing disturbance more specifically on stimulating warm-season grass coverage in addition to forbs would be valuable.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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**Ethics statement:** All research activities were approved by Colorado Parks and Wildlife's Animal Care and Use Committee (Project no. 02-2016).

**Data depository:** Analyses reported in this article can be reproduced using the data provided by Behney (2021).

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