NONBREEDING SEASON SURVIVAL AND HABITAT SELECTION OF NORTHERN BOBWHITE IN NORTHEASTERN COLORADO

by

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Northern bobwhites (*Colinus virginianus*) have experienced range-wide population declines and are listed as a Tier 2 species of conservation concern in Colorado. Recent harvest data from northeastern Colorado suggests bobwhite populations have declined and managers aim to identify the vital rates and habitat features by which population growth rate may be limited to guide management actions. Although many studies have suggested that bobwhite populations are most sensitive to changes in reproductive factors, recent work suggests that some populations can be sensitive to adult nonbreeding season survival. Additionally, northeastern Colorado has habitat and weather dynamics unique to the northern periphery of the northern bobwhite range. We monitored 157 bobwhites in northeastern Colorado for the 2019-2020 and 2020-2021 nonbreeding seasons to estimate nonbreeding season survival and habitat selection. This included constructing known-fate survival models for each study season to assess any variation in survival between the winter stages of early-winter (1-Oct to 19-Nov), mid-winter (20-Nov to 22-Jan), and late-winter (23-Jan to 31-Mar), as well as sex, age class, and mass at the time of capture. The best model for each season allowed weekly survival to vary among winter stages, with the period having the lowest survival corresponding with the harshest weather conditions. We also monitored bobwhite habitat selection by performing weekly covey habitat surveys. Predictor variables include vegetation cover percentages, micro-climate variables, vegetation structure variables, and species richness estimates at used and random sites. We then used stepwise backward selection modeling to determine if any variables being selected were disproportionate to their availability. Our final habitat selection model included visual obstruction, percent bare ground and percent litter cover. The coefficients were positive for each variable in the model. Winter survival was low in our study and dependent on weather conditions and predation. Habitat management has the potential to reduce the risk of nonbreeding season mortality for bobwhites, which is critical to sustain local populations at the northwestern edge of the species' range. Our research aims to provide demographic and habitat selection data to managers to assist them in management action decision making.

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Nonbreeding Season Survival of Northern Bobwhite in Northeastern Colorado

1.1 Introduction

Northern bobwhites (*Colinus virginianus*; hereafter, bobwhites) have experienced range wide population declines (Brennan 1991, Brennan 1994, Brennan and Kuvlesky 2005) and are listed as a Tier 2 species of conservation concern in Colorado (Colorado Parks and Wildlife 2015). Identifying the vital rates to which population growth rate is limited by, or sensitive to, can help guide management actions aimed to affect population size. For bobwhites, many studies have suggested that populations are most sensitive to changes in reproductive characteristics (Roseberry 1974, Klimstra and Roseberry 1975, DeMaso et al. 2011). However, some studies have suggested that populations can be sensitive to adult nonbreeding season survival. Folk et al. (2007) suggested a dependency on location; in the north, population growth rate was most sensitive to nonbreeding season survival in the earliest age class, whereas fertility was most influential in the South. In a meta-analysis using data from all over the United States, Sandercock et al. (2008) found that rate of population change was most sensitive to winter survival of adults. Winter survival varies dramatically among studies, regions, and years, and based on 21 studies, Sandercock et al. (2008) reported 6-month winter survival ranging from 4 to 52%. Over 5 years in Colorado, Snyder (1978) found Fall-Winter mortality ranged from 42 to

87%. To assess population limiting factors, demographic data must be available for all life-stages.

Although bobwhites are a popular gamebird and are heavily hunted in many states, roughly 1,800 hunters hunted bobwhites in Colorado in 2012, harvesting an estimated 3,811 birds (Colorado Parks and Wildlife 2012). For comparison, 44,885 hunters harvested 199,661 quail in Kansas in 2012 (Kansas Department of Wildlife, Parks, and Tourism 2015). On Tamarack State Wildlife Area in northeastern Colorado, harvest was as high as 699 quail in 1982 and as low as six in 2014 (Colorado Parks and Wildlife, unpublished data), suggesting high variation in population abundance.

Predators and exposure are the two main causes of natural mortality of bobwhites, with hunting playing less of a role. The main predators in northeastern Colorado along the South Platte River were bobcats (*Felis rufous*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and various avian predators. For bobwhites in the north, weather may severely affect survival rates (Robel and Kemp 1997) leading to highly variable survival between years. When temperatures decline, bobwhites have greater energy requirements and deep snow can limit the ability to reach, or entirely deprive bobwhites of food necessary to meet that requirement. The trade-off between avoiding predators and the need to forage is well documented (Lima 1986, Rogers 1987, Lima and Dill 1990) and harsh conditions can force birds to risk predation or starve. Carr and Lima (2014) even suggest that wintering birds may avoid sunlight, which is important for warmth, to avoid predators.

Although highly detailed bobwhite demographic and nest site selection information from the breeding season is available for northeastern Colorado, managers lack information on nonbreeding season survival or habitat selection. Therefore, the goal for this study was to estimate nonbreeding season survival of bobwhites with the objectives to (1) estimate survival in the nonbreeding season and (2) examine the causes of variation in survival. We predicted that survival would be low and determined by weather patterns due to the study area being at the far northwest corner of the bobwhite range.

1.2 Study Area

Our study was conducted from September to March 2019-2021 on Tamarack State Wildlife Area and Dune Ridge State Wildlife Area (SWA) in Logan County, Colorado (Figure 1.1). Details for Tamarack SWA have been reported in previous studies (Behney et al. 2020, Behney 2021). Tamarack SWA encompasses 4,533 ha along a 30-km stretch of the South Platte River while Dune Ridge SWA is a 151-ha, 2-km stretch. Both areas allow hunting and at Tamarack SWA, hunters must check-in, check-out, and self-report harvest and time spent hunting on a daily basis. The wildlife areas consist of river-bottom riparian forest near the river and upland rangeland/meadows further away from the river. The width of riparian habitat averages 0.7 km and the woodlands consist primarily of plains cottonwood (*Populus deltoides*) with an understory of western snowberry (*Symphoricarpos occidentalis*) and sandbar willow (*Salix exigua*), which are both useful cover for bobwhites. Based on vegetations samples taken during our study, the primary grasses and forbs that intermix with the understory include prairie cordgrass (*Spartina pectinate*), western wheatgrass (*Pascopyrum smithii*), reed canary grass *(Phalaris arundinacea),* smooth brome (*Bromus inermis*), switchgrass (*Panicum virgatum*), cheatgrass (*Bromus tectorum*), common ragweed (*Ambrosia artemisiifolia*), poison hemlock (*Conium maculatum*), and thistle (*Cirsium* spp.).

On Tamarack SWA, a large portion of the area to the south of the river-bottom is native sandsage (*Artemisia filifolia*) rangeland. Bobwhites use the edge habitat in the sandsage, but rarely travel beyond 0.5 km from the river-bottom. A portion of both Tamarack SWA and Dune Ridge SWA is upland meadows with interspersed food plots and tree rows of eastern red cedar (*Juniperus virginiana*) and Russian olive (*Elaeagnus angustifolia*) that have provided some expansion beyond the river-bottom (Snyder 1978).

The elevation of Tamarack SWA averaged 1,133 m and Dune Ridge SWA 1,211 m. Based on a 100-year climate summary for the area (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?co7513, accessed 15 March 2022), mean monthly precipitation during our study period (Oct – March) was 1.50 cm and mean monthly snowfall was 10.29 cm. Means of the monthly mean maximum and minimum temperatures during October to March during both years of our study were 9.93°C and -7.02°C, respectively. Means of the monthly mean temperatures during our study were higher than historical means (mean max. temp = 17.04°C, min. temp = -5.71°C), while precipitation was similar (mean monthly precip. = 1.26 cm, snowfall = 8.25 cm; https://ncdc.noaa.gov, accessed 19 Apr 2021).

1.3 Methods

1.3.1 Capture and Marking

We trapped bobwhites using baited walk-in traps (Stoddard 1931, Smith et al. 1981, Behney et al. 2020) from 6 September until 17 October 2019 at 288 trap locations, and 1 September to 23 October 2020 at 493 trap locations on Tamarack SWA and Dune Ridge SWA. Trap locations were spread throughout each property to achieve representation of all areas of the properties. Traps were moved if areas became saturated with radio-marked bobwhites or if no bobwhites were being caught. During the second season, we also used targeted night-lighting, where we tracked previously radio-marked birds at night to locate coveys and used spotlights and a hoop net to capture untagged birds.

Bobwhites were affixed with ≤ 6.5-g necklace-style VHF radio transmitters equipped with an 8-hour mortality sensor (American Wildlife Enterprises, Monticello, FL), which have been used frequently for bobwhites (Burger et al. 1995, DeMaso et al. 1997, Taylor et al. 1999a). We did not deploy transmitters on quail weighing less than 130 g to keep the transmitter mass less than 5% of the bird's body mass. Terhune et al. (2007) concluded that 6-g necklace style transmitters affixed on bobwhites weighing ≥ 132 g had no effect on survival. We captured 25 birds and three birds that were deemed lighter than the allowable weight to be fitted with transmitters in the first and second season, respectively. Furthermore, Behney (2021) found that bobwhites fitted with these transmitters during a previous study on Tamarack SWA exhibited demographic characteristics consistent with other published estimates. All captured bobwhites received a numbered aluminum leg band, were weighed, and sex and age were determined. After processing, birds were released at the site of capture. All trapping, handling, and marking procedures were consistent with the guidelines of the University of Nebraska, Institutional Animal Care and Use Committee (Project ID #1844).

1.3.2 Survival Monitoring

We attempted to assess status (live or dead) of all radio-marked bobwhites 4 or 5 times each week from October – March. When the transmitter's mortality sensor indicated a dead bird, we retrieved the transmitter and assessed cause of mortality (i.e., mammal, avian, hunter cripple, etc.). In the event a bird was no longer able to be located, we extensively searched the site and continued to monitor for it until the end of the season.

1.3.3 Statistical Analysis

Any deaths determined to be caused by the radio-collar (n=1) were excluded from analysis. We limited our sample to birds alive at the start of the nonbreeding season (October 1), and our nonbreeding season was six months, or 26 weeks, in length. We used single factor, known-fate models in Program MARK (White and Burnham 1999) to assess variation in weekly survival as predicted by categorical temporal effects, age, sex, and body mass at capture as covariates. We compared these models to a constant survival null model. Due to the differences in weather and habitat characteristics observed at different points in the season, early-winter (1-Oct to 19-Nov), mid-winter (20-Nov to 22-Jan), and late-winter (23-Jan to 31-Mar) (periods 1, 2, and 3) were used as categorical temporal effects. Early winter would be expected to have the highest weekly survival due to its typical mild weather, invertebrate availability, some live vegetation, and adults still in good body condition from the summer. However, during October and November there can still be relatively young, small subadults from late hatches that might be at higher risk for mortality. Late winter might typically have the lowest weekly survival due to harsher weather. We censored birds after they went missing from the site or transmitters were believed to be no longer functional. We used Akaike's Information Criterion (AIC_c) to rank the models (Burnham and Anderson 2002). Analysis was preformed separately for each year since annual weather conditions, sample size, and mortality patterns were substantially different.

1.4 Results

We included 157 bobwhites in our analysis. During our first season we included 11 birds that still had functional radio-collars from a previous breeding season study. The fates of birds in the first season were as follows: 18 survivals, 73 mortalities, 13 missing birds with unknown fates, and five transmitters deployed in the spring had the battery die. Five birds with transmitters and one with only a band were harvested by hunters. During the second season, zero survivals, 46 mortalities, two missing with unknown fates, and one defective collar with unknown fates were recorded. Five birds with transmitters were harvested by hunters.

The population of bobwhites appeared to be substantially lower during the second year of our study, and survival varied between years. For both seasons (2019-2020 and 2020-2021), we found that the temporal model with three periods during the season best explained variation in survival (w_i = 0.774 and w_i = 0.622, respectively; Table 1.1). Nonbreeding season survival in the 2019-2020 season (26 weeks) was $\hat{S}$ = 0.243 (95 % CI = 0.165–0.342). Weekly survival during each of the three time periods was $\hat{S}_1$ = 0.954 (95 % CI = 0.935–0.967), $\hat{S}_2$ = 0.917 (95 % CI =0.883–0.941), and $\hat{S}_3$ = 0.967 (95 % CI = 0.935–0.983). Seasonal survival was much lower during the second season (2020-2021) with $\hat{S}$ = 0.093 (95 % CI = 0.031–0.250). Weekly survival during each period was $\hat{S}_1$ = 0.931 (95 % CI = 0.901–0.953), $\hat{S}_2$ = 0.961 (95 % CI = 0.928–0.979), and $\hat{S}_3$ = 0.862 (95 % CI = 0.748–0.929). Sex, age, and body mass did not influence survival in either year of our study.

1.5 Discussion

1.5.1 Demography

Our nonbreeding season survival estimate is the first for bobwhite in Colorado, and our 26-week estimates for each of our two study seasons were 24.3% and 9.3%, respectively. Regional nonbreeding season estimates from Kansas, Iowa, and Illinois range from 4 to 37% (Robel and Kemp 1997, Madison et al. 2002). In a study at similar latitude in the northeastern corner of the bobwhite range, Lohr et al. (2011) found winter survival to be similar at 23%. Survival tends to be higher in southern regions but has been reported as low as 9% in Oklahoma (Parry et al. 1997). Sandercock et al. (2008) proposed that summer survival > 79% and winter survival > 52%, corresponding to an annual survival of 41%, is necessary to ensure viable bobwhite populations. These results indicate that the decline in bobwhite populations in northeastern Colorado can be partially attributed to nonbreeding season survival.

During the second season, we captured fewer bobwhites than during the first season despite increased effort and number of weeks spent trapping. This leads us to believe that the total bobwhite population was lower during the second season, which is supported by harvest data from Tamarack SWA. Despite spending more time hunting during the second season (395 vs. 436 hours), hunters harvested 66 bobwhites in the first season, five of which were radio-collared and five during the second season, three of which were radio-collared. We documented hunting mortalities in our radio-marked sample in addition to those reported in both seasons. In the first season we had one incident, and in the second season, two, in which we discovered dead bobwhites that were crippled and not recovered by the hunter.

1.5.2 Weather and Survival

We predicted early-winter would have the highest survival and late-winter the lowest due to differences in weather conditions. Such expected patterns were only met for the late winter period in the second year of study. However, we did find that the period with the lowest survival (period 2 in season one and period 3 in season two) corresponded with the period with the harshest weather (lowest daily average maximum and minimum temperatures, and most snowfall) in both seasons.

In February of 2021, northeastern Colorado was subject to a polar vortex, producing seven inches of snow and daily minimum temperatures as cold as -34.4^o C. During this nine-day period, all remaining birds in our sample died (n = 6), two of which due to exposure (full carcass, no external signs of injury), and four to predation. The average daily maximum and minimum temperatures for this period (late winter) during the second season were 7.87^o C and -6.17^o F, respectively, and total snowfall was 10 inches. On 26 October 2020, our study sites had the first snowfall of the season followed by the first sub-zero (F) daily minimum temperatures. In the two days following we had a six-bird die-off, four due to exposure and two to predation. We did not find any events where harsh weather mirrored bobwhite mortality in the first season, but it was also relatively milder with only one day of coinciding sub-zero temperatures and snow. Janke et al. (2017) found that lowest winter season survival rates over four years at multiple sites corresponded with the greatest snow accumulation, but evidence of effects of temperature on survival was marginal. Janke et al. (2017) also found that mortality due to weather was likely linked to increased vulnerability to predation and starvation rather than hypothermia in contrast to our findings. While we did not perform any necropsy in attempt to determine cause of death, the circumstantial occurrence of the short October 2020 event and the extreme cold of February 2021 event suggested that some birds likely died due to hypothermia.

1.5.3 Management Implications

Food plots or supplementary feeders may increase winter survival, especially during periods of harsh weather (Robel and Kemp 1997, Doerr and Silvy 2006). Food plots exist on Tamarack SWA, and a portion of the northern border is corn farmland. Bobwhites were observed in these plots during our study, suggesting that a more widespread implementation of food plots may be beneficial. Plots should focus on high nutrition and late year plants. Although these can be beneficial, any increase in food plots may be negated if predators or hunters focus their efforts nearby (Madison et al. 2002, Haines et al. 2004).

Periods of harsh winter weather and predation were the main causes of mortality on Tamarack SWA. Managers should focus habitat features that can protect bobwhites from these sources. Woody understory cover is well documented to be beneficial to bobwhites during the nonbreeding season, providing escape cover from predators, protection from snow and wind, and patches of bare ground (Roseberry et al. 1964, Roseberry and Klimstra 1984, Williams et al. 2000, Janke and Gates 2013, Perkins et al. 2014, Kroeger et al. 2020). In northeastern Colorado we found bobwhites selecting for visual obstruction, which can provide protection from predators, snow, and wind (Chamberlain et al. 2002), and bare ground that can provide surfaces for dusting, loafing, and forage (Stoddard 1931, Brown and Samuel 1978, Johnson and Guthery 1988). Litter may also supply food and favorable thermal conditions (Chamberlain et al. 2002) (Chapter 2). These landscape characteristics should all be monitored, maintained, and managed in areas where these are lacking on a large scale.

Our study, combined with data from a breeding season study in the region, provides parameters for use in population growth models to identify the most sensitive life-stages of bobwhites in northeastern Colorado. The nonbreeding season appears to be a critical part of the annual life cycle, and weather events such as those encountered in our second season are highly unpredictable. The complexities of management decisions for harvest or habitat should benefit from a holistic consideration of life stages to attempt to maximize growth during the life-stages considered to be most limiting to population growth.

Season	Model name	AIC_c	ΔAIC_c	w_i	*K*
2019-2020	Time	549.76	0.00	0.77	3
	Constant survival	554.14	4.37	0.09	1
	Sex	554.52	4.76	0.07	2
	Age	555.92	6.16	0.04	2
	Mass	556.14	6.37	0.03	2
2020-2021	Time	326.23	0.00	0.62	3
	Mass	329.29	3.06	0.13	2
	Constant survival	329.36	3.13	0.13	1
	Age	330.74	4.51	0.07	2
	Sex	331.37	5.14	0.05	2

Table 1.1: Number of parameters (*K*), corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i), and values used to rank models containing categorical temporal effects (time) or individual covariates hypothesized to affect the probability of nonbreeding season survival of northern bobwhite in northeastern Colorado, USA, 1 October 2019 – 31 March 2020 and 1 October 2020 – 31 March 2021.

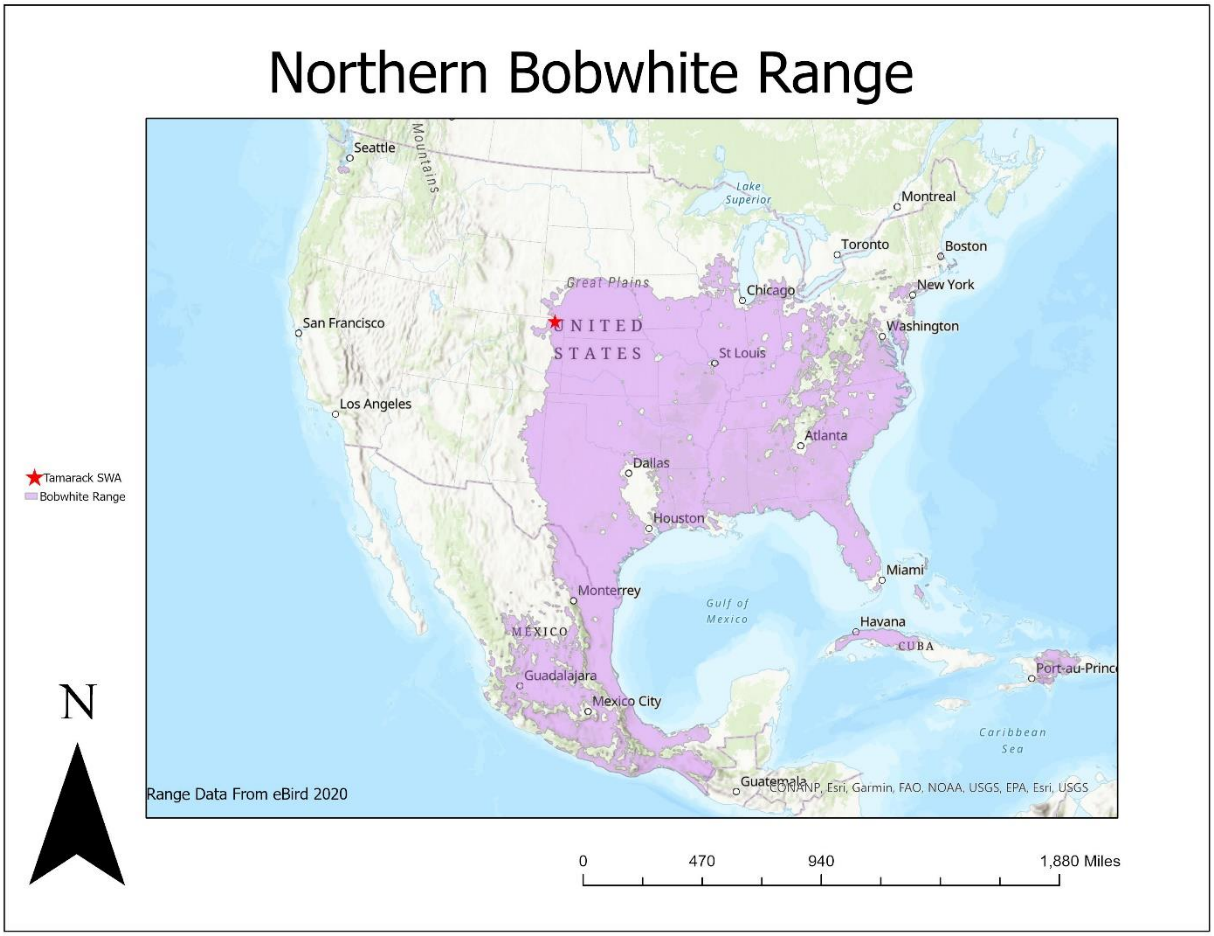

Figure 1.1: Northern bobwhite species distribution in North America. Purple indicates where bobwhites occur, and red star is the location of our study area. Map from eBird species count data.

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Chapter 2

Selection of Habitat by Northern Bobwhites Along a River Corridor in Northeastern Colorado

2.1 Introduction

Northern bobwhites (*Colinus virginianus*; hereafter, bobwhites) have experienced range-wide population declines (Brennan 1991, Brennan 1994, Brennan and Kuvlesky 2005) and are listed as a Tier 2 species of conservation concern in Colorado (Colorado Parks and Wildlife 2015). Habitat loss and degradation resulting from intensive agriculture, invasive species, and the lack of natural disturbances, have been identified as likely causes (Stoddard 1931, Roseberry et al. 1979, Roseberry and Klimstra 1984, Brennan 1994). For managers to be able to address these problems through habitat management, information is needed on what vegetation bobwhites are selecting for or against. Bobwhites require a diversity of vegetation types to accommodate their needs. Woody understory cover, bare ground, forbs, ground litter and grasses are all important for at least one life-stage (Roseberry et al. 1964, Snyder 1978, Taylor et al. 1999a). Identifying which of these are most important for each life-stage can help guide management actions.

For bobwhites, habitat has been shown to influence survival at both coarse and fine scales (Seckinger et al. 2008, Williams et al. 2000, Janke et al. 2015). Many studies have suggested that populations are most sensitive to changes in reproductive characteristics (Roseberry 1974, Klimstra and Roseberry 1975, DeMaso et al. 2011). However, other studies have suggested that populations can be sensitive to adult nonbreeding season survival. Folk et al. (2007) suggested a dependency on region for nonbreeding season survival. In a meta-analysis using data from throughout the United States, Sandercock et al. (2008) found that the rate of population change was most sensitive to winter survival of adults. To assess population limiting factors, habitat selection and use data must be available for all life-stages. Although highly detailed bobwhite demographic and nest site selection information from the breeding season is available for northeastern Colorado, managers lack information on nonbreeding season survival and habitat selection. Assessing habitat selection would help managers make management decisions that support the winter needs of bobwhites.

Although bobwhites are a popular gamebird and heavily hunted in many states, only about 1,800 hunters hunted bobwhites in Colorado in 2012, harvesting an estimated 3,811 birds (Colorado Parks and Wildlife 2012). For comparison, 44,885 hunters harvested 199,661 quail in Kansas in 2012 (Kansas Department of Wildlife, Parks, and Tourism 2015). Population levels of bobwhites are highly variable in Colorado, adding complexities for management decisions. For example, on Tamarack State Wildlife Area in northeastern Colorado, harvest was as high as 699 bobwhites in 1982, and as low as six in 2014 (Colorado Parks and Wildlife, unpublished data), suggesting high variation in population abundance.

In northeastern Colorado, bobwhites are generally limited to the South Platte River bottom riparian areas where there is abundant woody cover (Snyder 1978). Woody cover is important for protection from snow (Roseberry et al. 1964) and predators (Perkins et al. 2014). Outside of the river-bottom area, insufficient woody cover in the upland rangelands is thought to preclude use by bobwhites. However, in southeastern Colorado, bobwhites are regularly found in sandsage (*Artemisia filifolia*) rangelands far from river-bottom riparian areas. Tamarack State Wildlife Area (SWA) in northeastern Colorado is typical for the region; bobwhites are regularly observed in the river-bottom riparian area but are rarely observed in the upland rangelands. Approximately 2,700 ha of upland rangeland exist at Tamarack SWA. If woody cover is limiting the value of upland rangelands to bobwhites at Tamarack SWA then increasing woody cover may facilitate expansion of bobwhite range into the uplands. Facilitating use of uplands by bobwhites at Tamarack SWA would create an additional opportunity for hunters and potentially a more satisfactory hunting experience by spreading hunters through expanded areas and reducing current hunter concentrations in the river-bottom riparian area.

Traditionally, managers wishing to increase the amount of woody cover have relied on planting shrubs. Plums (*Prunus spp.*) are commonly planted in areas lacking woody cover to provide bobwhite habitat (Hiller et al. 2007, West et al. 2012, Pierce et al. 2016). However, this takes years to achieve desirable amounts of cover and is reliant on sufficient water for plant growth. An alternative strategy is to create artificial structures, which have been used successfully to establish bobwhite habitat (Webb and Guthery 1983, Boyer et al. 1989, Abbott 2003), but has not been implemented in northeastern Colorado. If bobwhites are observed using artificial structures, it would suggest that installing shrubs or structures themselves would be valuable methods to increase usable space for bobwhites into upland rangelands.

Our research goal was to assess winter habitat selection to better understand the full annual cycle of bobwhites in northeastern Colorado. Our objectives were to (1) determine if bobwhites selected for vegetation features disproportionate to their availability to focus management strategies for the area and (2) assess whether increasing woody vegetation through use of artificial structures in uplands could facilitate bobwhite range expansion.

2.2 Study Area

Our study was conducted from September to March 2019-2021 on Tamarack State Wildlife Area and Dune Ridge State Wildlife Area in Logan County, Colorado. Details for Tamarack SWA have been reported in previous studies (Behney et al. 2020 and Behney 2021). Tamarack SWA is comprised of 4,533 ha along a 30-km stretch of the South Platte River while Dune Ridge SWA is a 151-ha, 2 km-stretch. Both wildlife areas consist of river-bottom riparian forests near the river and upland rangeland/meadows further away from the river. The riparian habitat is on average 0.7 km wide and consists primarily of plains cottonwood (*Populus deltoides*), with an understory of western snowberry (*Symphoricarpos occidentalis*) and sandbar willow (*Salix exigua*). Based on vegetation samples taken during our study, the primary grasses and forbs that intermix with the understory include prairie cordgrass (*Spartina pectinate*), western wheatgrass (*Pascopyrum smithii*), reed canary grass *(Phalaris arundinacea)*, smooth brome (*Bromus inermis*), switchgrass (*Panicum virgatum*), cheatgrass (*Bromus tectorum*), common ragweed (*Ambrosia artemisiifolia*), poison hemlock (*Conium maculatum*), and thistle (*Cirsium* spp.).

On Tamarack SWA, a large portion of the area to the south of the river-bottom is native sandsage (*Artemisia filifolia*) rangeland. Bobwhites use the edge habitat in the sandsage, but rarely travel beyond ~0.5 km from the river-bottom. A portion of both Tamarack SWA and Dune Ridge SWA is upland meadows with interspersed food plots and tree rows of eastern red cedar (*Juniperus virginiana*) and Russian olive (*Elaeagnus angustifolia*), which provide some bobwhite range expansion beyond the river-bottom (Snyder 1978).

The elevation of Tamarack SWA averages 1,133 m and Dune Ridge SWA averages 1,211 m. Based on a 100-year climate summary for the area (https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?co7513, accessed 15 March 2022), mean monthly precipitation during our study period (Oct – March) was 1.50 cm and mean snowfall was 10.29 cm. Means of the monthly mean maximum and minimum temperatures during October to March during both years of our study were 9.93°C and -7.02°C, respectively. Means of the monthly mean temperatures during our study were higher than historical means (mean max. temp = 17.04°C, min. temp = -5.71°C), while precipitation was similar (mean monthly precip. = 1.26 cm, snowfall = 8.25 cm; https://ncdc.noaa.gov, accessed 19 Apr 2021).

2.3 Methods

2.3.1 Capture and Marking

We trapped bobwhites with baited walk-in traps (Stoddard 1931, Smith et al. 1981, Behney et al. 2020) from 6 September until 17 October 2019 at 288 trap locations, and 1 September to 23 October 2020 at 493 trap locations on Tamarack SWA and Dune Ridge SWA. Trap locations were spread throughout each property to achieve representation of all areas of the properties. Traps were moved as areas became saturated with bobwhites fixed with transmitters or if no bobwhites were being caught. In addition to walk-in traps, targeted night-lighting was used during the second season. We tracked previously radio-marked birds at night to locate coveys and used spotlights and a hoop net to capture untagged birds.

Bobwhites were affixed with ≤ 6.5 g necklace-style VHF radio transmitters equipped with an 8-hour mortality sensor (American Wildlife Enterprises, Monticello, FL), which have been used frequently for bobwhites (Burger et al. 1995, DeMaso et al. 1997, Taylor et al. 1999a). We did not deploy transmitters on bobwhites weighing less than 130 g to keep the transmitter mass less than 5% of the bird’s body mass. Terhune et al. (2007) concluded that 6 g necklace style transmitters affixed on bobwhites weighing ≥132 g had no effect on survival. We captured 25 birds and three birds that were deemed lighter than the allowable weight to be fitted with transmitters in the first and second season, respectively. Furthermore, Behney (2021) found that bobwhites fitted with these transmitters during a previous study on Tamarack SWA exhibited demographic characteristics consistent with other published estimates. All captured bobwhites received a numbered aluminum leg band, were weighed, and sex and age were determined. After processing, birds were released at the site of capture. All trapping, handling, and marking procedures were approved by the University of Nebraska, Institutional Animal Care and Use Committee (Project ID #1844).

2.3.2 Habitat and Microclimate Sampling

To assess habitat selection, we located each bird or covey monthly and then flushed them to get an exact location. Once a covey was flushed, we immediately sampled vegetation at the center of the flush point as well as at four random points in the same general habitat type within 200 m of the used location (i.e., within the distance bobwhites typically move in a day; Taylor et al. 1999a, Taylor et al. 1999b). At each used and random point, we visually estimated the percent coverage of bare ground, litter, and each vegetation species within a 1-m^2 sampling frame. We considered litter to be dead vegetation on the soil surface. In cases where species could not be determined, plants were identified to the lowest classification possible. Where snow was present, it was treated as its own cover type and its depth was measured to nearest centimeter. The tallest vegetation in the frame was measured and recorded to the nearest centimeter. We also noted the lowest five-centimeter mark visible on a 2.5-cm diameter pole, read from 4 m in four directions, 90° apart, from 1 m above the ground (Robel et al. 1970). At each sample point, a handheld

Kestrel weather meter was used to take temperature and wind speed at shoulder height and ground level.

2.3.3 Artificial Structures

In fall 2019, we created a line of artificial structures running perpendicular to the river-bottom where bobwhite inhabited out into the upland rangelands. It consisted of five large wooden cable spools with cedar and Russian olive branches stacked radially around them. Structures were ~5 m wide and ~1.5 m tall. The structures were spaced ~35 m apart along a ~150-m line.

The line of structures was walked once a week to look for bobwhites or signs of bobwhites, where the cover was hit with sticks to flush out bobwhites. We looked for any bobwhite signs (tracks or droppings) in or around the cover or if any radio-marked individuals were in or around the artificial structure. Searches in cover were exhaustive and invasive so we can assume that any bobwhites in the artificial cover would have been detected (detection probability = 1). We also searched an area where artificial cover was not deployed (i.e., control site). This control site was a designated unaltered area approximately the same size as the artificial cover and randomly placed in the same general area and cover type. We also recorded any events of bobwhites using the artificial structures during daily radiotelemetry locations.

2.3.4 Statistical Analysis

We evaluated two variables describing weather conditions, seven variables describing cover type and proportions, two variables describing the height and density of vegetation, and one variable quantifying the species richness at each sample site (Table 2.1). Due to stratification of cover types, our total cover estimates often resulted in a value greater than 100%. To keep samples consistent, we rescaled all cover values to have a total cover of 100%. We tested for collinearity of continuous variables using Pearson's correlation coefficients with a limit of $| r | < 0.7$ (Dormann et al. 2013). After cessation of trapping, we removed leftover bait and excluded any location data from within one week to the end of trapping from the habitat selection analyses to reduce trapping bait bias.

We created logistic regression generalized mixed models using glmmTMB package in R (R Core Team 2022) for our selection analysis to assess differences in site characteristics of used and random points. Sample identification and covey identification were used as random terms in all models to account for repeated sampling. We used backwards stepwise model selection (Doherty et al. 2010, Brooks et al. 2017) to remove uninformative variables by taking our global model and removing the single variable with the highest associated P-value with the test for a non-zero coefficient. We stopped when all variables in the reduced model had $P < 0.15$ (Bursac et al. 2008).

2.4 Results

We had 159 capture events using walk-in traps, catching 123 individuals during 2019 (the first capture season), and had 48 capture events with 43 individuals in 2020 (the second capture season). Ten additional individuals were captured via night-lighting in the second season. We radio tagged 98 individuals (43 females and 55 males) and 49 individuals (20 females and 29 males) in the first and second season, respectively. We included 110 total habitat surveys in our analysis.

Snow depth and percent snow cover, as well as windspeed at shoulder height and windspeed at ground level were correlated to each other above our defined limit. We chose to include snow depth and wind speed at ground level in future analyses due to their perceived biological importance. Percent snow cover and windspeed at shoulder height were excluded. Snow can hinder the ability to forage and thermoregulate and snow depth is a direct measurement of the amount of snow bobwhites must get through to forage, while shallow snow can produce percent cover values similar to another site with much greater depths. Wind speed at shoulder level may alter noise or interfere with flight, but given bobwhites are ground dwelling birds, wind speed at ground level is likely the condition more experienced.

Our final model to predict habitat selection (all $P < 0.15$) included height of visual obstruction, percent bare ground, and percent litter cover. The coefficients for relative probability of use were positive for each variable in the model (Figure 2.2; $\beta_{vis} = 0.02$, SE = 0.00, odds ratio [OR] = 1.02; $\beta_{bare} = 0.01$, SE = 0.01, OR = 1.01; $\beta_{litter} = 0.02$, SE = 0.01, OR = 1.01).

We observed limited selection of artificial cover. We found one bobwhite within 35 m of a structure during a daily radiotelemetry location, but none other during daily tracking. We did not detect any bobwhites or signs of bobwhites during weekly transects.

2.5 Discussion

2.5.1 Habitat Selection

Our results indicate that bobwhites were selecting for several vegetation characteristics disproportionate to their availability in northeastern Colorado. Average height of visual obstruction, percent litter cover, and percent bare ground cover at used sites was greater than at random sites for all three parameters, suggesting that bobwhites are selecting for areas with denser vegetation, and more bare ground and litter. The other vegetation and weather variables had measures similar at used and available (random) sites for birds in our sample.

The selection of areas with increased visual obstruction during the nonbreeding season is consistent with other studies (Kopp et al. 1998, Brooke et al. 2015). Visual obstruction can provide protection from predators, snow, and wind (Chamberlain et al. 2002). Patches of bare ground are also valuable to bobwhites, providing surfaces for dusting, loafing, and forage (Stoddard 1931, Brown and Samuel 1978, Johnson and Guthery 1988). Kopp et al. (1998) found that there was evidence of selection between 10–60% bare ground at flush points.

Chamberlain et al. (2002) found that bobwhites selected for roost sites with more litter cover, litter depth, and visual obstruction and suggests site vegetation structure is related to favorable thermal characteristics. We did not investigate nighttime roost sites, but we included thermal measures in our sampling design to evaluate this hypothesis. Our microsite weather variables did not vary between used and available sites, but our daytime microsite vegetation structure findings are consistent with those of Chamberlain et al. (2002). Bobwhites may be selecting for sites with denser vegetation and more litter during the daytime for reasons other than weather, or we may not have captured a weather metric that is important to bobwhite in our sampling.

Our results show a positive selection for litter cover, which contrasts with research that suggests that litter is less beneficial for bobwhites. Kuvlesky et al. (2002) concluded bobwhites select for areas with less litter cover and results from Peters et al. (2015) show that litter depth decreased survival. Other studies that included litter as a variable found it to not be a predictor of site selection (Brook et al. 2015, Unger et al. 2015), however these conflicting results may be due to the type of litter. Peters et al. (2015) contributed that *sericea lespedeza* dominated their study site, since its seeds are virtually indigestible by bobwhites and an accumulation of this litter has been associated with reduced forb establishment and species richness. In habitats such as pine stands, litter can be of complete coverage and composed of almost entirely pine needles, creating habitat of little value to bobwhites (Brennan 1991). In our study, litter mainly consisted of forbs and grasses that provide food, with a mean of 55.8% of coverage at used sites, and, while we did not take litter depth measurements, litter was relatively shallow (approximately ≤ 1 cm). This leads us to assume that differences in litter composition, cover, and depth can both alter and determine the value of litter to bobwhites.

Woody understory cover is well documented as important to bobwhites during the nonbreeding season, providing escape cover from predators, protection from snow and wind, and patches of bare ground (Roseberry et al. 1964, Roseberry and Klimstra 1984, Williams et al. 2000, Janke and Gates 2013, Perkins et al. 2014, Kroeger et al. 2020). Bobwhites were regularly documented using woody cover, so we were surprised to find that bobwhites in our study were not selecting for woody cover proportionately more than was available on the landscape. However, our random sites were chosen within 200 m of the used site, and the riparian area at Tamarack SWA and Dune Ridge SWA has abundant, relatively homogenous distributed woody cover. A landscape-level assessment would have certainly shown that bobwhites are strongly selecting for the woody, riparian areas on our study sites. In future studies it would be valuable to estimate the nearest distance to woody cover for investigating the spatial relationship between cover type and indirect selection. Kassinis and Guthery (1996) found that bobwhites landed in woody cover more than what is randomly available at the end of an escape flight and recommended that escape cover should be <100 m from any given point. Determining if bobwhites behave the same in our region, and if woody cover is adequately distributed, would be valuable to managers.

2.5.2 Management Implications

The artificial structures showed little to no signs of use. We located bobwhite in the sandhills within a quarter mile of the structures multiple times, suggesting the potential for limited use by our radio-marked birds. We hypothesize that woody cover is not currently limiting bobwhite populations on the river-bottom, where it is a limiting factor in the sandhills. Given the disparity in use between habitats and the lack of use of artificial structures, we assume that the river-bottom may not be fully saturated with bobwhites, meaning they have little need to expand their range. Focusing management on the already occupied habitat to increase survival of adults, nests, and broods may better utilize resources.

Periods of harsh winter weather and predation were the two main sources of mortality in northeastern Colorado (Chapter 1). While some habitat features can protect bobwhite from these sources (i.e., woody understory, denser vegetation, adequate areas for roosting, loafing, and foraging, and food), no amount of management can eliminate the effects of extreme weather events. Ritzell et al. (2022) found that in the southwestern U.S., where rainfall can account for a large portion of the annual variability in regional quail abundance, management could increase bobwhite population density beyond unmanaged land, but it could not stabilize inter-annual density. This may also be the case for northeastern Colorado, where management can dampen, but not eliminate risk of predation or the boom-bust cycle caused by extreme winter weather, especially when it extends over many days.

We found that, at a landscape scale, bobwhites are heavily dependent upon the woody habitat in the river corridor. Woody cover has been excluded from agricultural areas in the river corridor, so we encourage managers to maintain this unique habitat in the wildlife management areas. Our results suggest that litter, bare ground, and visual obstruction should all be monitored, maintained, and managed in areas where these are lacking on a large scale. Habitat management has the potential to reduce the risk of nonbreeding season mortality for bobwhites, which is critical to sustain local populations at the northwestern edge of the species' range.

Habitat and weather measures	**Mean, used sites**	**Mean, random sites**
Windspeed at ground (km/hr)	2.21	2.69
Temperature (°C)	9.99	10.09
Snow depth (cm)	0.25	0.30
Bare ground cover (%)	13.65	14.27
Litter cover (%)	55.82	50.35
Wood debris cover (%)	1.16	1.66
Grass cover (%)	22.80	29.74
Forb cover (%)	19.58	21.12
Woody cover (%)	15.86	13.20
Tallest plant height (cm)	137.37	112.44
Visual obstruction (cm)	57.26	40.46
Species richness (n)	3.62	3.64

Table 2.1: Means of variables at used sites and random sites included in nonbreeding season habitat selection analysis of northern bobwhites in northeastern Colorado, USA, 1 October 2019 – 31 March 2020 and 1 October 2020 – 31 March 2021.

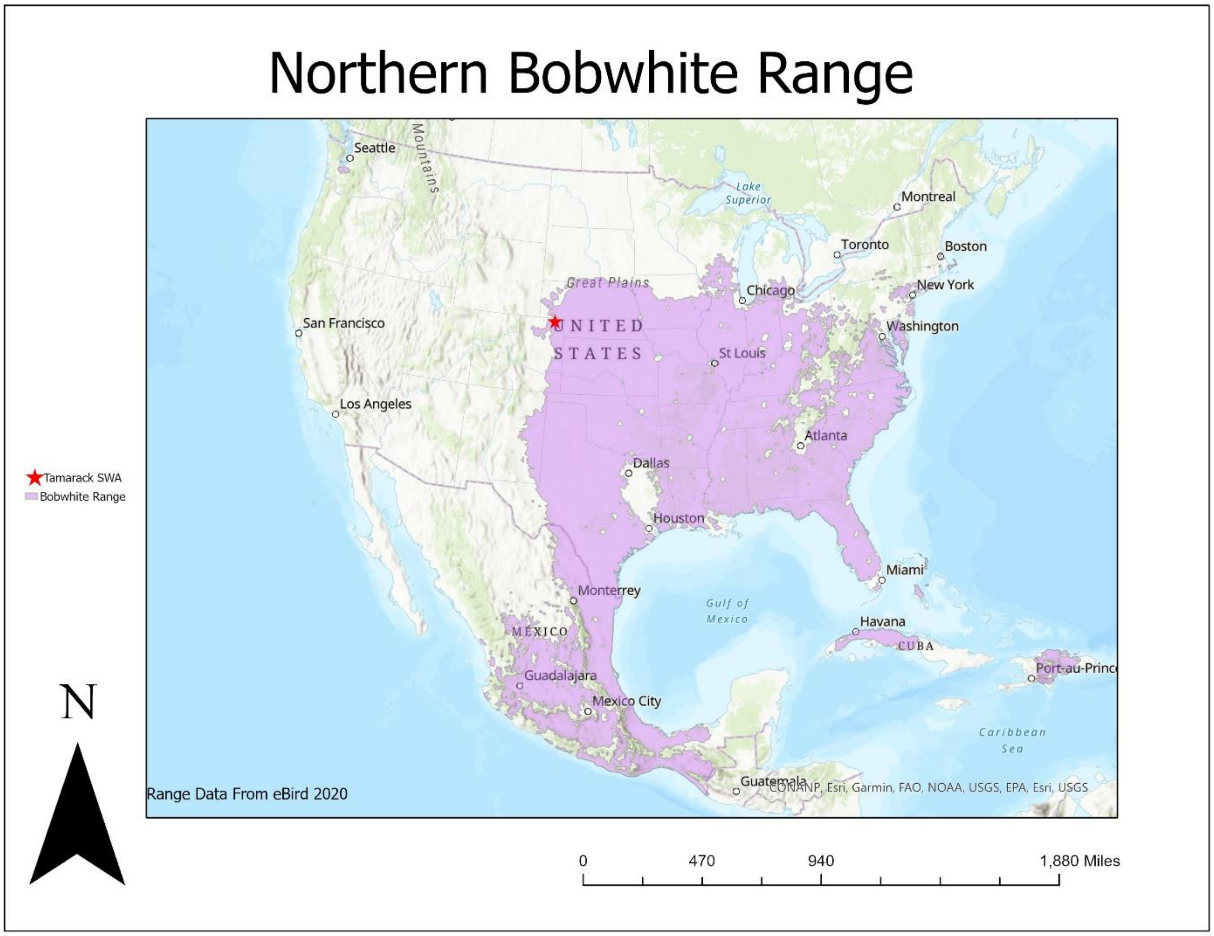

Figure 2.1: Northern bobwhite species distribution in North America. Purple indicates where bobwhites occur, and red star is the location of our study area. Map from eBird species count data.

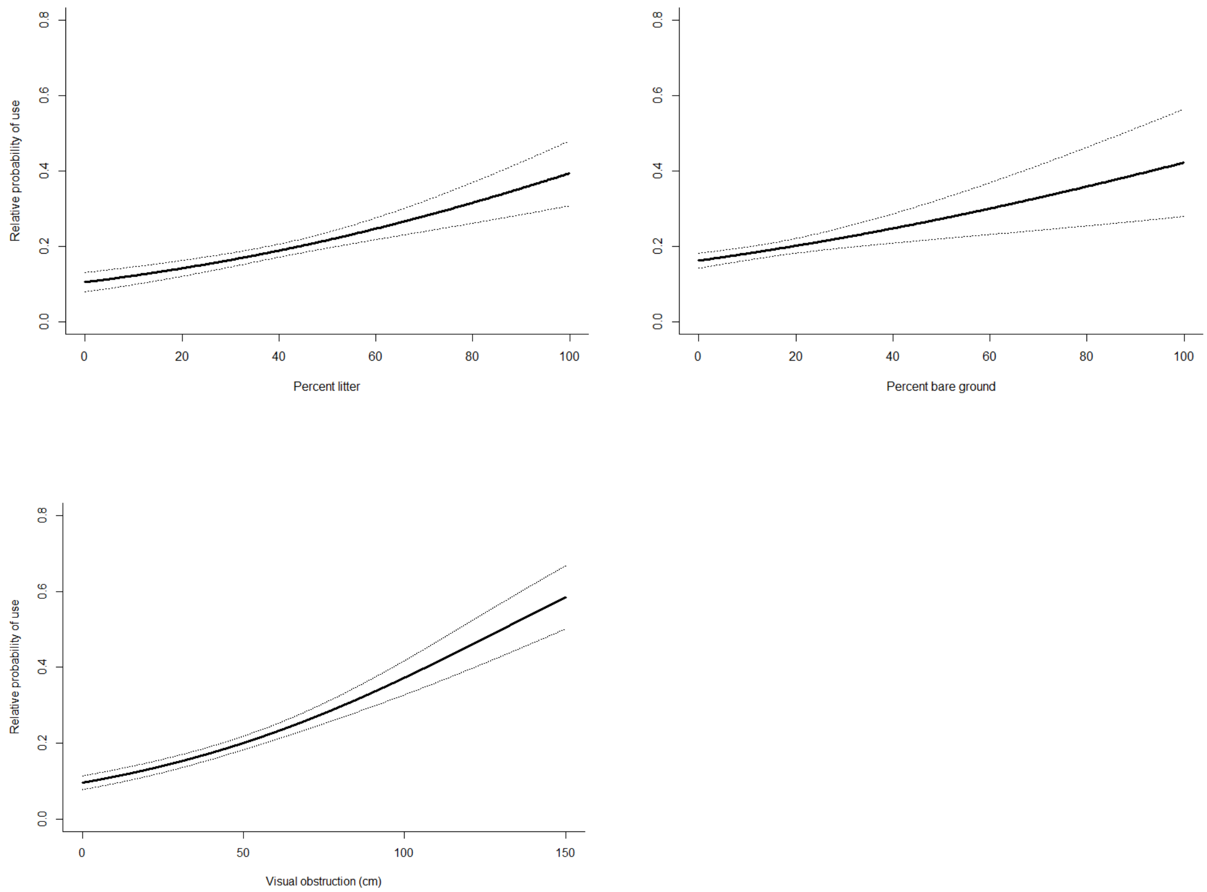

Figure 2.2: Predicted relative probability of use for northern bobwhite nonbreeding season site selection as a function of percent litter, percent bare ground, and average height of visual obstruction (cm) in northeastern Colorado, USA, 1 October 2019 – 31 March 2020 and 1 October 2020 – 31 March 2021. Visual obstruction was estimated from a Robel pole read at four points 90^{o} apart. Dotted lines represent confidence interval of 1 SE.

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