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# EFFECT OF FOOD DISTRIBUTION ON RESOURCE SELECTION OF NORTHERN BOBWHITE

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## ABSTRACT

Supplemental feeding is a common management tactic used to increase survival and reproduction of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite). Different supplemental feeding methods alter the distribution of resources across a landscape in unique ways and may influence the space use and resource selection of target species differently. Predators may concentrate their movements near fed sites, and different distributions of supplemental feed may encourage bobwhite to concentrate their movements closer to feed than other areas, thereby altering the potential for predator-prey interactions near feed. We used radio-tracked locations and movements in areas with stationary feeders (“feeder fed”) and nonsupplementally fed (“unfed”; study 1, year 1) or nonstationary “broadcast fed” (study 2, year 2) areas to compare resource selection within a Bayesian framework. Second- and third-order resource selection functions indicated bobwhite were more likely to occur in proximity to feeders and feedlines when available, but bobwhite resource selection was more strongly affected by feeders. These results demonstrate that different distributions of food resources can affect prey resource selection, potentially altering the probability of overlap between nontarget predator and target prey species. Managers of bobwhite populations should broadcast feed instead of using feeders to avoid concentrations of bobwhites, which may lead to reduced survival.

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**Key words:** *Colinus virginianus*, home range, northern bobwhite, resource selection, supplemental feed

The distribution of resources across a landscape has a fundamental influence on many ecological processes. The movement patterns and distribution of both predator and prey are driven in large part by the distribution of resources (Sih 1982, Boyd 1996), thus contributing to the distribution of predation risk. The heterogeneous dispersion of risk and resource patches then affects risk-dependent decision making. According to optimal foraging theory, prey must weigh the cost of predation against the reward of potential resources gained when selecting resource patches (Kamil and Sargent

1981). Individuals may leave patches earlier and accept lower gains when foraging in areas perceived to have high predation risk (Brown 1992, Kotler 1997, Lima 1998), or as the quality of foraging patch increases, prey may be more willing to endure higher levels of predation risk, especially if they have high resource demands such as during juvenile growth or the production of eggs (Abrahams and Dill 1989, Lima 1998). Consequently, it is important to consider how management practices that alter the distribution of resources may alter managed prey species’ resource selection.

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Supplemental feeding artificially alters the distribution of food within a landscape and is often used in an effort to increase the survival or reproductive rates of target species (Hawkins 1937, Townsend et al. 1999, Godbois et al. 2004, Guthery et al. 2004, Turner et al. 2008). However, some predators are more likely to appear near supplementally fed sites than expected (Godbois et al. 2004, Turner et al. 2008), and there is concern about potential unintended effects on target populations (Doonan and Slade 1995, Godbois et al. 2004, Guthery et al. 2004, Turner et al. 2008, Henson et al. 2012). Additionally, different distribution techniques may affect predator and prey selection of fed areas in unique ways. Using feeders can attract prey to small, fixed spaces and may result in concentrated movements of both predator and prey near feeders. In contrast, broadcasting feed across a large area gives prey the opportunity to forage more naturally (Kassinis and Guthery 1996, Buckley et al. 2015, Miller et al. 2017). Consequently, predators may also be less likely to forage in small, concentrated areas. Thus, different feeding techniques may uniquely alter the distribution of risk, resulting in differences in resource selection patterns that could influence the potential for predator-prey interactions.

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) are fast-paced, ground-dwelling birds endemic to the United States, and a widely popular game species (Guthery et al. 2004). Their populations have been declining across the majority of their historical range for the past several decades (Stoddard 1931, Brennan 1991, Hernández et al. 2013), and they are now a species of conservation concern. Land managers use supplemental feeding in an attempt to increase population survival and reproduction rates, though it produces mixed results (Townsend et al. 1999, Sisson et al. 2000, Guthery et al. 2004, Haines et al. 2004, Rollins et al. 2006). While evidence suggests supplemental feeding may improve bobwhite survival (Sisson et al. 2000, Townsend et al. 1999), increased perceived risk may affect target species' resource selection, resulting in sublethal effects that may impact survival later on (Lima and Dill 1990, Sheriff et al. 2009, Mohlman et al. 2019). Most research on the impacts of supplemental feed on bobwhite occurs in the fall and winter (Townsend et al. 1999, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Buckley et al. 2015). However, bobwhite use supplemental feed during the summer despite an abundance of natural food sources (Miller et al. 2017, Wellendorf et al. 2017), and the distribution of supplemental feed and the subsequent distribution of risk are likely to impact breeding individuals.

Our objective was to determine how two different methods of distributing supplemental feed affected the resource selection of bobwhite. We compared bobwhite resource selection within 2 separate experiments. In the first, parameters of interest were compared between unfed treatment containing empty feeders and a feeder-fed treatment containing filled feeders (hereafter, study 1). In the second, parameters of interest were compared between a broadcast-fed treatment and a feeder-fed treatment (hereafter, study 2).

We hypothesized that bobwhite need to expend less energy to access feed near feeders than to find and exploit natural food sources in the unfed treatment, making supplemental feed a higher quality resource (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Buckley et al. 2015, Wellendorf et al. 2017). Consequently, we predicted bobwhite in the feeder-fed treatment would select areas closer to feeders within the feeder-fed treatment than in the unfed treatment.

To our knowledge, there are no studies directly comparing resource selection of broadcast-fed and feeder-fed wild bobwhite. Previous studies show both feeding methods sometimes reduce home range size and concentrate and localize coveys (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Wellendorf et al. 2017). Thus, we hypothesized that because feeders distribute feed within a small, fixed space while feedlines require bobwhites to move across larger areas to access grain, bobwhite would need to expend less energy to access feed near feeders than near feedlines and would view areas near feeders as a higher quality resource. Given that there are enough feeders <200 m apart to ensure multiple feeders are accessible to each individual within a resident bobwhite population, we predicted resource selection would differ between treatments. More specifically, we predicted bobwhites would select for areas closer to feeders than they would to feedlines.

## STUDY AREA

Di-Lane Wildlife Management Area is managed for the growth of early successional vegetation with a management emphasis on bobwhite. This area is located in the Upper Coastal Plain of Burke County, Georgia, USA and is made up of roughly 3,300 ha of federally owned land. Prominent species of vegetation and land cover types included a mixture of fallow fields (mostly camphorweed [*Heterotheca subaxillaris*], common ragweed [*Ambrosia artimisiifolia*], partridge pea [*Chamaecrista fasciculata*], annual low panicgrasses [*Dichanthelium* spp.], and perennial broomsedge [*Andropogon virginicus*] and split-beard bluestem [*Andropogon ternarius*]), loblolly pine uplands (*Pinus taeda*), hardwoods (mostly oak [*Quercus* spp.], hickories [*Carya* spp.], sweetgum [*Liquidambar styraciflua*], and black gum [*Nyssa sylvatica*]), and dove field plantings (Clearfield® sunflowers [*Helianthus* spp.], wheat [*Triticum aestivum*], and browntop millet [*Urochloa ramosa*]). The Georgia Department of Natural Resources (DNR) burned the pine uplands and disked fallow fields on rotation every 2–4 years and implemented biannual meso-mammal predator control and year-round supplemental feeding of sorghum (*Sorghum bicolor*). Average temperatures for Burke County ranged from 31.6–15° C in May and 33.3–19.4° C in June–August. Average rainfall was approximately 6.4 cm in May and ranged from 12.6–13.4 cm in June–August (NOAA National Climatic Data Center 2019).

## METHODS

### Experimental Design

A total of 223 feeders, initially installed in 2008, were an average of 175 m apart within our treatments throughout both study years to minimize the distance among all available feeders. Most feeders were within patches of scrub shrub and covered with medium to high density vegetation on all sides. The Georgia DNR distributed all supplemental feed within feeders and along feedlines.

*Study 1: unfed vs. feeder-fed treatments.*—We randomly assigned the feeder-fed treatment to a treatment area on the eastern half of the property (1,501 ha) and filled all feeders within the treatment ( $n = 131$ ) with sorghum on 12 June 2018. The unfed treatment was assigned to a treatment area on the western half (1,501 ha) and all feeders within the treatment ( $n = 92$ ) were emptied of any remaining feed and left in place on the same day (Figure 1). The fill level of 10 random feeders within the fed treatment was checked every week.

*Study 2: feeder-fed vs. broadcast-fed treatments.*—Supplemental feed was distributed via feeders within the eastern treatment area to create a feeder-fed treatment and via feedlines within the western treatment area to create a broadcast-fed treatment using the same study area boundaries as the previous year (Figure 1). We checked the fill level of 10 random feeders within the feeder-fed treatment every week, and feeders were refilled when necessary. Beginning 20 May 2019, sorghum was broadcast along predetermined routes spaced an average of 100–300 m apart along preexisting roads and firebreaks. The spreader used in this study spread feed directly behind the machine (i.e., on the road or firebreak) and into the adjacent cover. Feed was spread once every 2 weeks as described by Buckley et al. (2015) along approximately 63 km of feed lines at a rate of 5.38 bushels/ha and at an average width of 13 m.



Fig. 1. Feeding treatments of northern bobwhite (*Colinus virginianus*) on Di-Lane Wildlife Management Area, Burke County, Georgia, USA. Treatment 1 indicates the unfed treatment in 2018 and the broadcast-fed treatment in 2019. Treatment 2 indicates the feeder-fed treatment in both years.

Feeders were full within the broadcast-fed treatment during turkey hunting season, between 21 March and 15 May 2019, to continue supplemental feeding of bobwhite while complying with Georgia law that prohibits turkey hunting over bait. Nearly all feeders within the broadcast treatment were empty following turkey season; only 11 of 92 feeders were still filled with seed in early July. Feed was removed from the 11 feeders and all others within the treatment were checked and verified to be empty.

### Trapping and Processing

Stoddard funnel traps baited with sorghum were uniformly placed underneath dense vegetative cover 250–300 m apart throughout feeding treatments (Stoddard 1931). Trapping occurred over the course of 2 weeks in late February–early March (2018–2019). All individuals were weighed, sexed, aged, and given unique number leg bands (National Band and Tag Co. Newport, KY, USA) upon capture. Individuals with a body mass  $\geq 130$  g were fitted with very high frequency (VHF) radio-transmitters (Holohil Systems, Carp, Ontario, Canada and American Wildlife Enterprises, Monticello, FL, USA). Caution was taken to deploy transmitters equally across the study site and within feeding treatments. Between 60–100 radio-tags were deployed within a given trapping session. Transmitters had an estimated battery life of 10–12 months and emitted a mortality signal when transmitters remained stationary for greater than 12 hours. Radio-collared bobwhites left over from another study within the same study area were also included in our sample (Mohlman et al. 2019). All bobwhite trapping and tagging was carried out under Georgia DNR collecting permits and institutional approvals (Animal use protocol #A2019 06-018-Y3-A0).

### Radio-telemetry

Bobwhite were relocated 5–7 days/week using Biotracker receivers and 3-element directional antennae from Lotek Wireless Inc. (Newmarket, Ontario, Canada) via homing telemetry (White and Garrott 1990, Amelon et al. 2009). Locations were taken approximately 20–30 m from individual bobwhites at varying times of the day to minimize disturbance and account for possible variation in diurnal resource selection. Bobwhite found in the same location 3 days in a row were relocated from within 3–5 m of the bird to visually confirm whether the individual was incubating a nest. Upon finding a nesting bird, technicians relocated nesting birds each morning until the nest either hatched or failed. Nest fate was visually confirmed by technicians. Individuals with broods were tracked daily and flushed at 14 and 21 days after hatch to confirm the presence of chicks. Global Positioning Systems (GPS) were used to obtain observer locations, and compasses were used to determine the azimuth to the bobwhite.

### Statistical Analysis

To ensure that analyses only included data collected when supplemental feed was being reliably distributed within each

designated treatment, only data gathered between 12 June 2018–1 September 2018 and 20 May 2019–7 September 2019 were used in analyses. Bobwhites did not travel to other designated feeding treatments outside of their assigned treatment for the duration of each experiment. Data collected for bobwhites within each year were analyzed separately for ease of computation and interpretation.

All analyses were conducted within a Bayesian framework using R (R Core Team 2019) and R package ‘jagsUI’ (version 1.5.2, <https://github.com/kenkellner/jagsUI>, accessed 10 Dec 2019). All posterior distributions of model parameters were estimated using Markov chain Monte Carlo (MCMC). Three MCMC chains were generated for each analysis using varying numbers of adaptation, iteration, and burn-in values, and a thinning rate of 10 to obtain successful chain convergence and an adequate effective sample size to characterize the posterior distributions. We determined that a model successfully converged when R-hat values, which compare between- and within-chain variation values, were  $<1.1$  (Gelman et al. 2004). Values of all estimated parameters had an R-hat value of  $\leq 1.1$ , and further visual inspection of trace plots confirmed chain convergence. We reported posterior means, 95% and 50% credible intervals [CrIs], and Bayesian  $P$ -values for parameters of interest. The Bayesian  $P$ -values denote the probability of effect existence by calculating the Maximum Probability of Effect, which is equivalent to the proportion of the posterior distribution with the same sign as the mean (Makowski et al. 2019). We determined an effect to be of negligible size when the entirety of 89% of the highest density interval of the posterior distribution was within a region of practical equivalence (ROPE) ranging from  $-0.025$ – $0.025$  (Kruschke 2014). Partial overlap between the ROPE and posterior distribution indicated that effect significance was undecided (Kruschke 2014). As a general rule, only effects relating directly to our hypotheses and those in which  $>97.5\%$  of the posterior distribution did not overlap the ROPE were mentioned in our results.

## Resource Selection Function

To estimate the study species’ selection of supplementally fed areas and scrub shrub and forest edge, which function as escape cover and may influence selection of fed sites (Stoddard 1931, Wiseman and Lewis 1981, Johnson and Guthery 1988, Taylor and Burger 2000), we used a resource selection function (RSF) to analyze the distance of used (telemetry relocations) and available (randomly generated) locations to the closest feature of each resource (Manly et al. 2002). Scrub shrub and forest edge were classified using the land cover classification methods described in Gardner (2020). We modeled RSFs at second- (i.e., selection of home ranges) and third-order (i.e., selection of resources within each home range) scales as described by Johnson (1980). Adequate area coverage is important when available locations are being generated (Buskirk and Millspaugh 2006). Because using equal numbers of available points to sample each home range may not equally sample all home ranges, we chose to incorporate the 5:1 ratio of available:used points used in discrete choice modeling as outlined by Cooper and Millspaugh (1999, 2001) to sample relevant areas.

Home ranges were estimated to determine availability at the third-order selection scale (Appendix A). We generated random points within each individuals’ home range equal to 5 times the number of telemetry relocations recorded for each individual. For second-order selection, we created a minimum bounding polygon surrounding all used locations of bobwhites within each treatment using the ‘Minimum Bounding Geometry’ tool in ArcGIS (release 10.7, Esri, Inc., Redlands, CA, USA, 2019) and buffered the polygons to enlarge them by the bobwhites’ average daily movement distance. The area was enlarged to avoid missing possible areas that bobwhites could have explored but not detected. Euclidean distance to each land cover type of interest (forest edge, scrub shrub, and feeder or feedline, depending on treatment) for all used and available locations was then calculated using the ‘Generate Near Table’ tool in ArcGIS.

We analyzed resource selection using separate logit models and included covariates for sex, nesting status, and brood rearing status along with distances to resources of interest (Taylor et al. 1999, Taylor and Burger 2000). Random intercepts were included to account for successive telemetry locations and individual variation in responses to feeding treatments (Gillies et al. 2006, Coppes et al. 2018). Random slopes further account for individual variation in treatment effects (Gillies et al. 2006); however, presumably due to small sample size, we were unable to obtain model convergence when we incorporated both.

We assigned normal distributions to random effects with a mean of 0 and with vague gamma-distributed precision terms ( $1/\text{variance}$ ). We used vague normal priors for fixed effects (mean = 0, standard deviation [SD] = 0.001). Distance-related numerical predictors were divided by 10 to make a more meaningful output. Nondistance-related numerical predictors were scaled using the ‘scale’ package of base R to standardize measurements for comparison and decrease time until convergence. The model was parameterized using the “effects” parameterization, where the fixed effects represented the difference in resource selection from either the unfed control treatment (year 2018) or the broadcast fed treatment (year 2019) and the feeder-fed treatment as follows:

$$\text{logit}(p_i) = \beta_{0,j} + \beta_{1,j} \times X_1 + \beta_{2,j} \times X_2 + \dots + \beta_{k,j} \times X_k$$

where,  $use_i \sim \text{Bern}(p_i)$  is the model likelihood and

$$\beta_k \sim \text{Norm}(p_k, \tau_k);$$

$$p_k \sim \text{Norm}(0, 0.001);$$

$$\tau_k \sim \text{Gamma}(0.1, 0.1)$$

The model was fitted for  $i = 1, 2, \dots, N$  where  $N$  represents the total number of observations,  $j = 1, 2, \dots, n$  denotes the number of individuals, and  $k = 1, 2, \dots$  denotes the number of fixed effects. Here  $use$  represents the probability of use for each individual  $j$ .  $\beta_0$  represents the random intercept of each individual.  $\beta_i$  represents the coefficient estimated from fixed effect predictors  $X_i$  described in Table 1.

Table 1. Description of covariates used in resource selection function analyses in 2018 and 2019.

Covariate	Description
SS	Distance to scrub shrub (m)
Edge	Distance to forest edge (m)
Treatment	Feeding treatment
Nest	Whether individual was classified as nesting
Brood	Whether individual had a brood
Sex	Male or female
Feed	Distance to nearest feeder or feedline depending on treatment (m)
Feed * Sex	Interaction between distance to nearest fed area and sex
Feed * Treatment	Interaction between distance to nearest fed area and treatment
Feed*SS	Interaction between distance to nearest fed area and distance to scrub shrub
Feed*Edge	Interaction between distance to nearest fed area and distance to forest edge
Feed * Nest	Interaction between distance to nearest fed area and nesting status
Feed * Brood	Interaction between distance to nearest fed area and brood status
Feed * Edge * Treatment	Interaction between distance to nearest fed area, distance to forest edge, and treatment
Feed * SS * Treatment	Interaction between distance to nearest fed area, distance to scrub shrub, and treatment

Table 2. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) second-order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Intercept	-0.44	-0.26	-0.16	-0.07	0.12	0.87	-
Sex	-1.19	-1.01	-0.91	-0.82	-0.63	1.00	-
SS	-0.43	-0.34	-0.29	-0.24	-0.15	1.00	0.00
Edge	-0.02	0.01	0.03	0.04	0.07	0.89	44.98
Treatment	-0.57	-0.38	-0.28	-0.18	0.01	0.97	-
Nest	-1.07	-0.89	-0.78	-0.69	-0.49	1.00	-
Brood	-0.36	-0.07	0.08	0.23	0.52	0.63	-
Feed	-0.09	-0.08	-0.07	-0.07	-0.06	1.00	0.00
Feed * Sex	0.05	0.06	0.07	0.07	0.08	1.00	0.00
Feed * Treatment	-0.01	0.00	0.01	0.01	0.02	0.75	100.00
Feed * Nest	0.04	0.05	0.05	0.06	0.07	1.00	0.00
Feed * Brood	-0.03	-0.01	0.00	0.01	0.03	0.57	98.77
Feed * SS	-0.01	-0.01	-0.01	0.00	0.00	0.92	100.00
Feed * Edge	-0.01	-0.01	-0.01	0.00	0.00	1.00	100.00
Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.85	100.00
Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.52	100.00

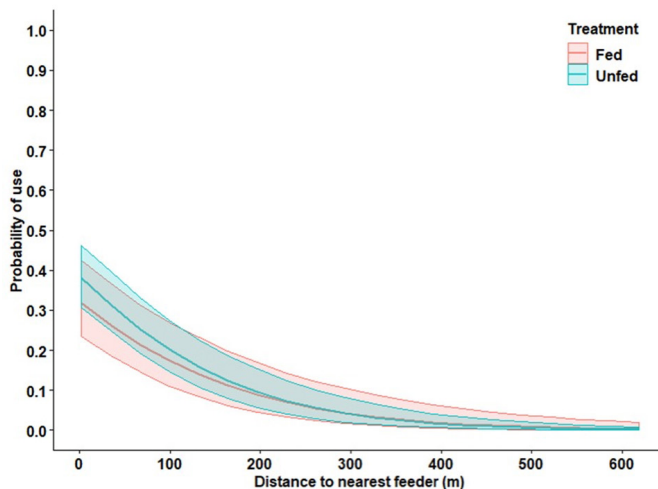


Fig. 2. Second-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.

## RESULTS

### Study 1: Unfed vs. Feeder-fed Resource Selection

Twenty-six individuals were used in our analyses of year 2018 data, 14 (8 female [F], 6 male [M]) of which were within the unfed treatment while the remaining 12 (7 F, 5 M) were within the feeder-fed treatment. It was unlikely that treatment affected probability of use of feeders on the landscape scale (Table 2, Figure 2); however, for every 10-m increase in distance to feeder, probability of use decreased by 7% (Bayesian  $P$ -value = 1.00; Table 2). In addition, for every 10-m increase in distance to scrub shrub, probability of use decreased by 33% (Bayesian  $P$ -value = 1.00; Table 2). Within their 90% kernel home ranges, the interaction between treatment and distance to feed had a somewhat small effect on probability of resource use, where for every 10-m increase in distance to feeder, probability of use decreased by 4% regardless of treatment (Bayesian  $P$ -value = 1.00; Table 3, Figure 3). Additionally, for every 10-m increase in distance to scrub shrub, probability of use decreased by 31% (Bayesian  $P$ -value = 1.00; Table 3). Within their 50% kernel utilization distributions (KUD) core use areas, bobwhites selected for areas closer to feeders within the feeder-fed treatment (Bayesian  $P$ -value = 1.00; Table 3), whereas bobwhites within the unfed treatment were much more likely to select for areas farther from feeders than feeder-fed bobwhite (Figure 4).

### Study 2: Broadcast vs. Feeder-fed Resource Selection

Thirty-five bobwhite were included in our RSF analyses, 19 (9 F, 10 M) of which were within the broadcast-fed treatment while the remaining 16 (9 F, 7 M) were within the feeder-fed treatment. On all selection scales, bobwhites selected for areas closer to feed, but were more likely to select for areas closer to

feeders than feedlines (Bayesian  $P$ -value = 1.00 for all; Tables 4, 5), though the effect size of the interaction between distance to feeder and treatment was somewhat small within their 50% core use areas (Figures 5–7). In addition, bobwhites selected for areas closer to scrub shrub on all scales, where for every 10-m increase in distance to scrub shrub, probability of use decreased by 26% on the landscape scale (Bayesian  $P$ -value = 1.00, Table 4), by 21% within their 90% home ranges (Bayesian  $P$ -value = 1.00; Table 5), and by 23% within their core use areas (Bayesian  $P$ -value = 1.00; Table 5).

## DISCUSSION

We found support for our hypothesis stating the resource selection of feeder-fed and broadcast-fed bobwhites would differ. Bobwhites on all measured selection scales selected for areas closer to fed sites; however, bobwhites were more likely to select for areas closer to feeders than feedlines. In agreement with previous studies, this result suggests bobwhite viewed areas near supplemental feed as higher quality foraging patches regardless of the abundance of natural food resources or distribution method (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Miller et al. 2017, Wellendorf et al. 2017). This is likely because consuming supplemental feed allows bobwhites to meet their energy demands more quickly than when utilizing natural food patches (Whitelaw et al. 2009, Miller et al. 2017). However, given that feed is more concentrated underneath feeders and does not diminish as time passes as it does along feedlines so long as the feeder is filled (McLaughlin et al. 2017), feeders may have been viewed as higher quality patches compared to natural food sources than feedlines. Our results suggest bobwhites have a higher probability of being closer to feeders than feedlines, potentially increasing their risk of interacting with predators focusing their foraging efforts near feed. As a result, future research should explore the survival implications of feeder use versus feedline use.

Evidence supported our hypotheses that resource selection of feeder-fed and unfed bobwhites would differ between treatments, though our predictions did not match all results. While bobwhites established their home ranges closer to feeders regardless of treatment, bobwhites within the feeder-fed treatment were more likely to select for areas closer to feeders within their home ranges and core use areas than those in the unfed treatment. This result suggests bobwhites are likely to forage near feeders (Johnson 1980) and may view fed sites as higher quality foraging patches than available natural resource patches. It is uncertain why unfed bobwhites selected for areas closer to feeders, but individuals may have established their home ranges prior to our study when all feeders had been full. Assuming individuals viewed areas near feeders as higher quality resource patches, resource selection may reflect past selection preferences. Additionally, the distance among feeders (<200 m apart) was such that bobwhites likely were making second-order decisions that go

Table 3. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) third-order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Kernel %	Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.04	-0.86	-0.75	-0.66	-0.47	1.00	-
	Sex	-0.94	-0.74	-0.64	-0.53	-0.34	1.00	-
	SS	-0.37	-0.27	-0.22	-0.17	-0.07	1.00	0.00
	Edge	-0.03	0.00	0.02	0.03	0.06	0.78	63.39
	Treatment	-0.31	-0.10	0.01	0.12	0.33	0.53	-
	Nest	-1.33	-1.13	-1.02	-0.91	-0.72	1.00	-
	Brood	-0.52	-0.21	-0.05	0.11	0.41	0.59	-
	Feed	-0.05	-0.04	-0.04	-0.03	-0.02	1.00	8.76
	Feed * Sex	0.03	0.05	0.05	0.06	0.07	1.00	0.00
	Feed * Treatment	-0.03	-0.02	-0.01	0.00	0.01	0.85	96.32
	Feed * Nest	0.05	0.07	0.07	0.08	0.09	1.00	0.00
	Feed * Brood	-0.02	0.00	0.01	0.02	0.04	0.70	87.22
	Feed * SS	-0.02	-0.01	-0.01	0.00	0.00	0.96	100.00
	Feed * Edge	-0.01	-0.01	-0.01	-0.01	0.00	1.00	100.00
	Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.74	100.00
Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.52	100.00	
50%	Intercept	-3.17	-2.90	-2.76	-2.63	-2.36	1.00	-
	Sex	0.41	0.68	0.82	0.96	1.24	1.00	-
	SS	-0.25	-0.13	-0.07	-0.01	0.11	0.78	17.56
	Edge	-0.10	-0.04	-0.02	0.01	0.06	0.65	49.37
	Treatment	0.95	1.21	1.35	1.49	1.76	1.00	-
	Nest	0.05	0.27	0.39	0.51	0.73	0.99	-
	Brood	-0.29	0.10	0.31	0.52	0.90	0.85	-
	Feed	0.09	0.11	0.12	0.13	0.14	1.00	0.00
	Feed * Sex	-0.09	-0.07	-0.06	-0.05	-0.04	1.00	0.00
	Feed * Treatment	-0.13	-0.11	-0.10	-0.09	-0.08	1.00	0.00
	Feed * Nest	-0.05	-0.04	-0.03	-0.02	-0.01	1.00	30.14
	Feed * Brood	-0.06	-0.03	-0.02	-0.01	0.02	0.85	58.72
	Feed * SS	-0.04	-0.03	-0.03	-0.03	-0.02	1.00	18.27
	Feed * Edge	0.00	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * Edge * Treatment	-0.04	-0.03	-0.03	-0.03	-0.02	1.00	5.56
Feed * SS * Treatment	0.01	0.02	0.03	0.03	0.04	1.00	49.03	



Table 4. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) second-order resource selection in relation to feeder-fed and broadcast-fed treatments in 2019. Intercept denotes the effect of the broadcast-fed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Intercept	-1.34	-1.23	-1.17	-1.11	-1.00	1.00	-
Sex	-0.17	-0.05	0.01	0.07	0.18	0.55	-
SS	-0.30	-0.26	-0.23	-0.21	-0.17	1.00	0.00
Edge	0.02	0.03	0.04	0.05	0.07	1.00	5.72
Treatment	0.26	0.40	0.47	0.55	0.69	1.00	-
Nest	-0.30	-0.09	0.02	0.12	0.34	0.54	-
Brood	-0.05	0.10	0.17	0.24	0.38	0.94	-
Feed	-0.02	-0.02	-0.01	-0.01	0.00	0.97	100.00
Feed * Sex	-0.01	0.00	0.00	0.01	0.01	0.55	100.00
Feed * Treatment	-0.11	-0.09	-0.09	-0.08	-0.07	1.00	0.00
Feed * Nest	-0.03	-0.01	-0.01	0.00	0.02	0.66	98.80
Feed * Brood	-0.04	-0.03	-0.02	-0.02	0.00	0.99	90.87
Feed * SS	0.00	0.00	0.00	0.01	0.01	0.99	100.00
Feed * Edge	-0.02	-0.02	-0.01	-0.01	-0.01	1.00	100.00
Feed * Edge * Treatment	0.02	0.02	0.02	0.03	0.03	1.00	64.54
Feed * SS * Treatment	-0.02	-0.01	-0.01	-0.01	0.00	1.00	100.00

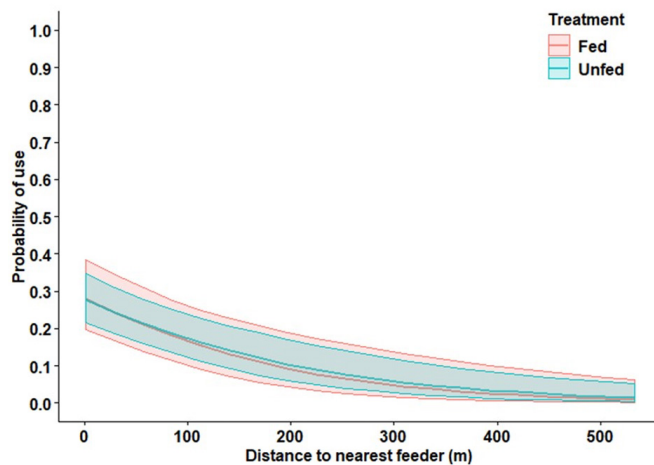


Fig. 3. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 90% home ranges.

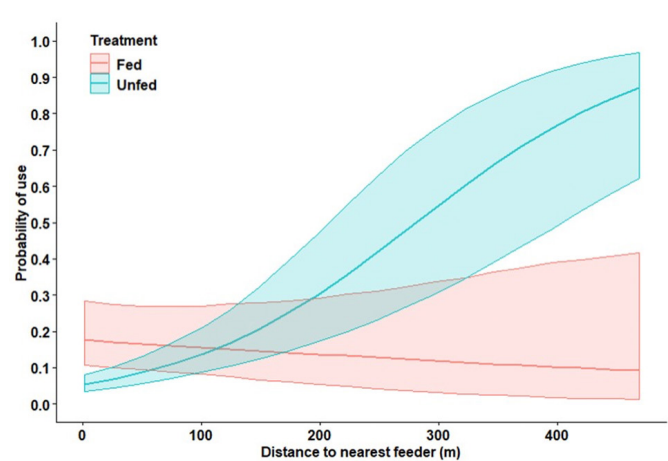


Fig. 4. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 50% core use areas.

Table 5. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) third-order resource selection in relation to feeder-fed and broadcast-fed treatments in 2019. Intercept denotes the effect of the broadcast-fed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.48	-1.36	-1.30	-1.24	-1.12	1.00	-
	Sex	-0.14	-0.01	0.06	0.12	0.25	0.71	-
	SS	-0.27	-0.22	-0.19	-0.16	-0.12	1.00	0.00
	Edge	-0.06	-0.04	-0.03	-0.02	0.00	0.98	37.49
	Treatment	0.21	0.38	0.47	0.55	0.70	1.00	-
	Nest	-0.84	-0.60	-0.49	-0.37	-0.14	1.00	-
	Brood	-0.64	-0.49	-0.41	-0.33	-0.18	1.00	-
	Feed	-0.03	-0.02	-0.01	-0.01	0.00	0.97	96.64
	Feed * Sex	-0.02	-0.01	0.00	0.00	0.01	0.64	100.00
	Feed * Treatment	-0.08	-0.07	-0.06	-0.06	-0.04	1.00	0.00
	Feed * Nest	0.02	0.05	0.06	0.07	0.09	1.00	0.00
	Feed * Brood	0.03	0.04	0.05	0.06	0.07	1.00	0.00
	Feed * SS	0.00	0.01	0.01	0.01	0.01	1.00	100.00
	Feed * Edge	-0.01	-0.01	-0.01	0.00	0.00	1.00	100.00
	Feed * Edge * Treatment	0.01	0.01	0.01	0.01	0.02	1.00	100.00
Feed * SS * Treatment	-0.01	0.00	0.00	0.01	0.01	0.74	100.00	
50%	Intercept	-1.61	-1.46	-1.39	-1.31	-1.17	1.00	-
	Sex	-0.13	0.02	0.10	0.18	0.33	0.80	-
	SS	-0.30	-0.24	-0.21	-0.17	-0.11	1.00	0.00
	Edge	-0.06	-0.03	-0.02	-0.01	0.01	0.89	61.70
	Treatment	-0.05	0.15	0.25	0.36	0.56	0.95	-
	Nest	-0.70	-0.46	-0.33	-0.21	0.03	0.96	-
	Brood	-0.54	-0.37	-0.26	-0.16	0.02	0.96	-
	Feed	-0.03	-0.01	-0.01	0.00	0.01	0.80	100.00
	Feed * Sex	-0.03	-0.01	-0.01	0.00	0.01	0.78	100.00
	Feed * Treatment	-0.06	-0.04	-0.03	-0.03	-0.01	1.00	21.81
	Feed * Nest	0.00	0.03	0.04	0.05	0.07	0.98	20.73
	Feed * Brood	0.00	0.02	0.03	0.04	0.06	0.99	25.04
	Feed * SS	0.00	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * Edge	-0.01	-0.01	-0.01	-0.01	0.00	1.00	100.00
	Feed * Edge * Treatment	0.01	0.01	0.01	0.01	0.02	1.00	100.00
Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.59	100.00	

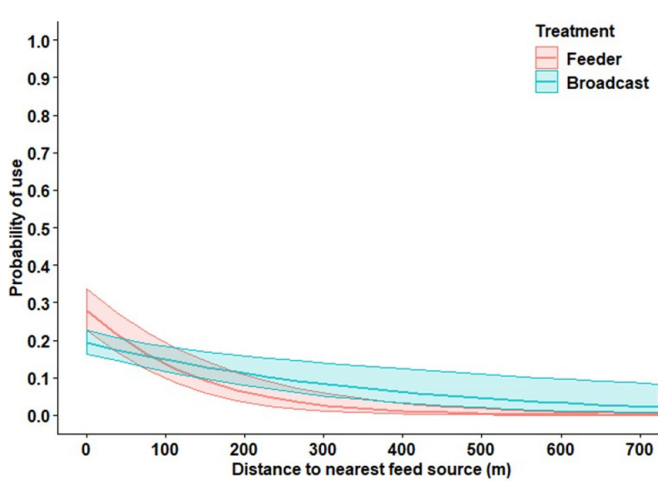


Fig. 5. Second-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019.

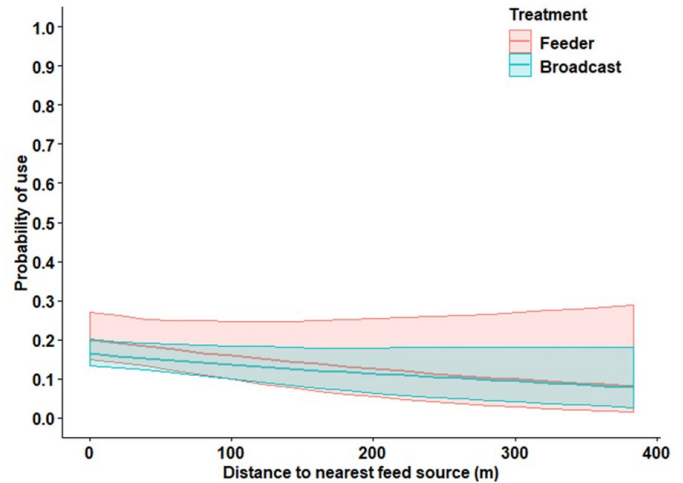


Fig. 7. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 50% core use areas.

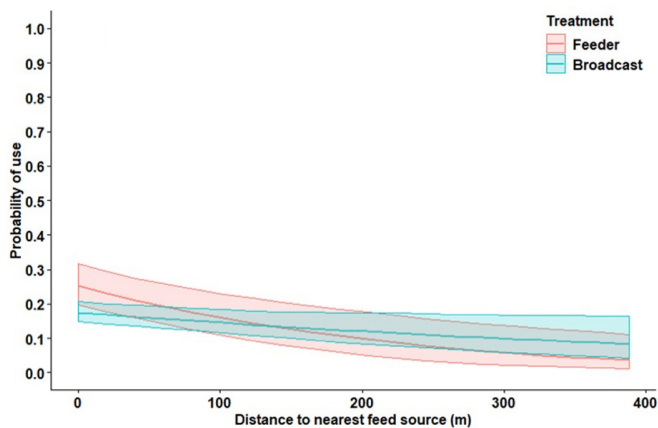


Fig. 6. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 90% home ranges.

beyond the distance between feeders (i.e., they could not avoid them). Moreover, the effects of the feeders that were filled with feed were more apparent at the third order. Regardless, an increase in concentration near feeders may increase the overall probability of predators focusing their foraging efforts near feeders.

The spatial context of the feed source location with respect to scrub shrub and forest edge did not play a role in selection of fed areas. However, distance to scrub shrub had a relatively strong impact on bobwhite resource selection in both study years at most selection scales. Bobwhites are likely to incorporate scrub shrub into their home ranges for its value as escape cover and for protection against weather extremes (Stoddard 1931, Wiseman and Lewis 1981, Johnson and Guthery 1988, Taylor and Burger 2000). Bobwhites can also increase their use of woody cover as level of perceived risk rises (Mohlman et al.

2019). While we did not compare bobwhite selection of scrub shrub between treatments, it is possible that an increase in predator concentration near fed areas may influence bobwhite use of woody cover. Researchers interested in investigating the effect of different feed distributions on predator-prey relationships and risk-dependent behavior may benefit from investigating use of scrub shrub by bobwhites when exposed to different feeding treatments.

Due to the pseudoreplicated nature of the study, treatment effects may be confounded with site effects, and differences in selection may be attributable to differences in landscape configuration and resource availability between treatments instead of differences in supplemental feed distribution. However, taken collectively, our results imply different distributions of food resources can impact breeding season resource selection of bobwhites. Bobwhite were more likely to be closer to feeders than feedlines, potentially increasing their comparative risk of encountering predators foraging near feed. Even so, the full extent of the effect of different supplemental feed distribution methods on bobwhite needs further investigation. We were unable to determine whether bobwhites faced greater levels of perceived risk in either treatment, which could impact subsequent behavior and resource selection associated with nesting and brood-rearing behaviors (Lima and Dill 1990). In addition, we were unable to determine differences in bobwhite survival rates between treatments. Increased movement has been associated with increased predation rates (Sisson et al. 2000), and the increased movement of bobwhites foraging along feedlines may have a greater negative impact on survival than feeders. However, as there are many nontarget species that utilize supplemental feed besides bobwhites that may act as buffer prey (Guthery et al. 2004, Henson et al. 2012), overall risk of bobwhite predation may decrease near feed (Davis 1957). Additionally, nest depredation of ground-nesting species can increase in

supplementally fed areas (Cooper and Ginnett 2000, Hamilton et al. 2002, Selva et al. 2014), and the distribution of predators near feed may alter the potential for nest predation. Finally, the distribution of supplemental feed may impact the resource selection of individuals during times of resource scarcity such as in the fall and winter. Future research should attempt to quantify the effect of food distribution on the behavior, survival, and subsequent population dynamics of species of interest through the evaluation of fine-scale movement and resource selection of nesting birds, brood-rearing individuals, and winter coveys.

## MANAGEMENT IMPLICATIONS

Managers for bobwhite populations with objectives that include bobwhite harvest and stakeholder satisfaction typically have to intensify their management to be successful. Supplemental feeding is one tool in the manager's toolbox to raise carrying capacity in food-limited systems. Managers should broadcast feed instead of using feeders to avoid overly concentrated use by bobwhites that may lead to reduced survival. Given that we observed weak biological effects of feed on space use, concerns over baiting should be minimal. Legal, financial, and ethical considerations should be a part of the decision process regarding supplemental feeding.

## ACKNOWLEDGMENTS

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## APPENDIX A. BOBWHITE HOME RANGE ANALYSIS

We estimated fixed kernel density home ranges (50% and 90% contours) of bobwhites using r package “adehabitatHR” (Worton 1989, Börger et al. 2006, Calenge 2006). Although the least-squares cross-validation (LSCV) method is recommended for bandwidth selection in ecological studies (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999), bobwhites often spent several consecutive days in the same location when they were nesting, and our home range estimates did not converge using this method. Instead, we used a single smoothing parameter ( $h$ ) that was iteratively chosen based on successive trials to produce what visually appeared to be the most accurate home ranges. Accuracy was determined using several criteria: 1) inclusion of all observed locations, 2) no holes in the home range except in areas of open water, and 3) not excessively large. For example, given that we tracked the birds daily and bobwhites are not known to move large distances and return in a short amount of time, it would be unrealistic to include areas >500 m away from observed locations within a season. Bobwhite home ranges are commonly estimated for only those individuals with  $\geq 25$ –30 relocations following the recommendations of Seaman et al. (1999) and Kenward (2001) (Terhune et al. 2010, Singh et al. 2011, McGrath et al. 2017). However, given that we did not use the LSCV method, we attempted to identify the minimum number of locations necessary to obtain an accurate home range estimate by graphing home range area curves to visually determine when each curve reached an asymptote (Odum and Kuenzler 1955, Bond et al. 2001). Bobwhite home ranges reached an asymptote with a minimum of 30 locations within study 1. Study 2 home ranges reached an asymptote with a minimum of 50–55 locations, but <10 individuals had enough relocations for home range estimation. In order to preserve sample size for greater statistical power, we chose to defer to the existing literature and analyzed data of individuals with  $\geq 30$  locations in both field seasons.

Along with treatment, we included covariates that would be likely to influence home range size such as sex (Taylor et al.

1999), reproductive status (with nest, with brood, or neither), and number of locations used in home range estimation (Macdonald et al. 1980). Both feeders and feedlines were placed unevenly across the property, and in 2019, 12 of the 92 feeders within the broadcast fed treatment were mistakenly overlooked and left full for a large portion of the field season. To quantify whether bobwhites had the potential to have been regularly using space that contained supplemental feed, we visually confirmed the appearance of any overlap between all 90% home range polygons and supplementally fed areas using ArcGIS (release 10.7; Esri, Redlands, CA, USA, 2019). All home range polygons within fed treatments overlapped with supplemental feed; however, home ranges of 2 bobwhite in the broadcast-fed treatment overlapped with both feed lines and filled feeders. As a result, we included whether an individual had been exposed to multiple feeding styles as an additional parameter in the home range analyses of bobwhite in the 2019 field season.

We performed a separate linear regression using a log-normal distribution within a Bayesian framework for each year. We used vague normal priors for fixed effects (mean = 0, precision = 0.001), and numerical predictors were scaled using the scale package of base R to standardize measurements and allow for comparison. The model was parameterized using the “effects” parameterization where the fixed effects represented the difference from either the unfed control treatment (year 2018) or the broadcast fed treatment (year 2019) as follows:

$$\mu_j = \beta_0 + \beta_{j,treatment} + \beta_{j,sex} \times X_{sex} + \beta_{j,nest} \times X_{nest} + \beta_{j,brood} \times X_{brood} + \beta_{j,loc\_freq} \times X_{loc\_freq},$$

Where  $HRsize_i \sim dlnorm(\mu_j, \tau)$  is the model likelihood and

$$\tau \sim Gamma(0.1, 0.1);$$

$$\beta_k \sim Norm(\mu_k, \tau_k);$$

$$\mu_k \sim Norm(0, 0.001);$$

$$\tau_k \sim Gamma(0.1, 0.1)$$

are model priors. The model was fitted for  $j = 1, 2, \dots, n$ , where  $n$  denotes the number of individuals, and  $k = 1, 2, \dots$  represents the number of fixed effects. Here  $HRsize$  represents the home range size for individual  $j$ .  $\beta_0$  represents the intercept.  $B_{treatment}$  represents the effect of feeding treatment.  $B_{sex}$  characterizes the effect of sex.  $B_{nest}$  symbolizes the effect of nest status.  $B_{brood}$  symbolizes the effect of brood status.  $\beta_{loc\_num}$  characterizes the effect of the number of locations used to estimate home range.  $X$  represents the response variable for each respective fixed effect noted.

## Bobwhite Home Range Results

*Study 1: feeder-fed treatment vs. unfed treatment.*—Twenty-six bobwhite were included in our home range and core use area analyses. Fourteen individuals (8 F, 6 M) were within the unfed treatment while the remaining 12 (7 F, 5 M) were within the feeder-fed treatment. Bobwhite home ranges

(90% KUDs) within the feeder-fed treatment were 16% larger than those in the unfed treatment (Bayesian  $P$ -value = 0.92, Tables A1, A2). Home ranges of nesting individuals and individuals that had broods were 63% and 43% smaller, respectively, than individuals that were recorded with neither (Bayesian  $P$ -value = 0.99, 0.97, respectively, Table A1). Male home ranges were 28% larger than female home ranges (Bayesian  $P$ -value = 0.99, Tables A1, A3), and for every 6 locations included in home range estimates, home range size increased by 8% (Bayesian  $P$ -value = 0.86, Table A1).

Bobwhite core use areas (50% KUDs) within the feeder-fed treatment were 11% larger than those in the unfed treatment (Bayesian  $P$ -value = 0.86, Tables A1, A2). Core use areas of nesting individuals and individuals that had broods were 126% and 73% smaller, respectively, than for individuals that were recorded with neither (Bayesian  $P$ -value = 1.00, 1.00, respectively, Table A1). Male core use areas were 8% larger than female core use areas (Bayesian  $P$ -value = 0.79, Tables A1, A3). For every 6 locations included in core use area estimates, core use area size increased by 10% (Bayesian  $P$ -value = 0.92, Table A1).

*Study 2: feeder-fed treatment vs. broadcast-fed treatment.*—Thirty-five bobwhites were included in our home range analyses. Nineteen individuals (9 F, 10 M) were within the broadcast-fed treatment while the remaining 16 (9 F, 7 M) were within the feeder-fed treatment. Bobwhite home ranges were 31% smaller within the feeder-fed treatment than the broadcast-fed treatment (Bayesian  $P$ -value = 0.98, Tables A1, A2). Male home ranges were 39% larger than female home ranges (Bayesian  $P$ -value = 1.00, Tables A1, A3). No other parameters of interest were likely to have affected home range size, including whether individuals had a nest or brood (Bayesian  $P$ -value = 0.57, 0.61, respectively, Table A1), or the locations included in home range estimation (Bayesian  $P$ -value = 0.70, Table A1).

Bobwhite core use areas were 26% smaller within the feeder-fed treatment than within the broadcast-fed treatment (Bayesian  $P$ -value = 0.95, Tables A1, A2). Male home ranges were 28% larger than female home ranges (Bayesian  $P$ -value = 0.95, Tables A1, A3), and nesting individuals had 36% smaller home ranges than those that had neither nested nor had a brood (Bayesian  $P$ -value = 0.78, Table A1). No other parameters of interest had a clear effect on home range size, including whether individuals had a brood (Bayesian  $P$ -value = 0.63, Table A1), or the number of locations included in home range estimation (Bayesian  $P$ -value = 0.58, Table A1).

Table A1. Mean linear regression output and credible intervals for northern bobwhite (*Colinus virginianus*) home range sizes in relation to feeder-fed and unfed treatments in 2018 and broadcast-fed and feeder-fed treatments in 2019. Intercept denotes the effect of the unfed (2018) or broadcast-fed (2019) treatment on females.

Year	Kernel %	Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value
2018	50%	Intercept	1.91	2.23	2.39	2.56	2.87	1.00
		Treatment	-0.10	0.04	0.11	0.18	0.33	0.86
		Nesting	-1.23	-0.93	-0.79	-0.64	-0.33	1.00
		Brood	-0.95	-0.69	-0.56	-0.42	-0.14	1.00
		Sex	-0.14	-0.01	0.06	0.13	0.29	0.79
		Location Freq	-0.05	0.05	0.09	0.14	0.24	0.92
	90%	Intercept	2.71	3.03	3.18	3.34	3.66	1.00
		Treatment	-0.06	0.08	0.15	0.22	0.37	0.93
		Nesting	-0.92	-0.63	-0.49	-0.35	-0.06	0.99
		Brood	-0.75	-0.49	-0.36	-0.23	0.03	0.97
		Sex	0.04	0.18	0.25	0.33	0.46	0.99
		Location Freq	-0.07	0.03	0.08	0.12	0.22	0.86
2019	50%	Intercept	1.55	1.93	2.12	2.32	2.70	1.00
		Treatment	-0.52	-0.32	-0.23	-0.14	0.05	0.95
		Nesting	-1.12	-0.57	-0.31	-0.04	0.50	0.78
		Brood	-0.45	-0.19	-0.06	0.07	0.32	0.63
		Sex	-0.02	0.16	0.25	0.34	0.52	0.96
		Location Freq	-0.33	-0.13	-0.03	0.07	0.28	0.58
	90%	Intercept	2.69	3.03	3.20	3.37	3.70	1.00
		Treatment	-0.53	-0.36	-0.27	-0.19	-0.02	0.98
		Nesting	-0.80	-0.30	-0.06	0.19	0.66	0.57
		Brood	-0.29	-0.07	0.05	0.16	0.38	0.61
		Sex	0.09	0.25	0.33	0.41	0.56	1.00
		Location Freq	-0.34	-0.16	-0.07	0.02	0.21	0.70

Table A2. Summary of northern bobwhite (*Colinus virginianus*) home ranges within each feeding treatment in 2018 and 2019; SD is standard deviation.

Year	Kernel %	Treatment	<i>n</i>	Mean	SD	Lower range	Upper range
2018	90	Unfed	14	25.27	6.87	15.48	38.87
		Feeder-fed	12	27.88	7.78	14.86	39.21
	50	Unfed	14	7.10	2.43	4.48	11.26
		Feeder-fed	12	7.45	1.98	3.61	12.43
2019	90	Broadcast-fed	19	41.63	12.10	21.92	64.21
		Feeder-fed	16	32.19	11.26	12.95	53.27
	50	Broadcast-fed	19	11.56	3.43	6.11	19.02
		Feeder-fed	16	10.14	3.88	3.70	16.27

Table A3. Summary of male (M) and female (F) northern bobwhite (*Colinus virginianus*) home ranges in 2018 and 2019; SD is standard deviation.

Year	Kernel %	Sex	<i>n</i>	Mean	SD	Lower range	Upper range
2018	90	M	11	30.17	5.91	21.28	39.21
		F	15	23.77	7.14	14.86	38.86
	50	M	11	7.54	1.98	5.28	11.41
		F	15	7.05	2.43	3.61	12.43
2019	90	M	17	43.84	11.18	20.15	64.21
		F	18	31.16	9.87	12.96	41.3
	50	M	17	12.65	3.60	5.49	19.02
		F	18	9.26	2.94	3.70	14.02

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