

EFFECT OF FOOD DISTRIBUTION ON RESOURCE SELECTION OF PREDATOR  
AND PREY

by

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(Under the Direction of JOHN C. MAERZ and JAMES A. MARTIN)

ABSTRACT

Management actions that alter the dispersion of food resources may alter target and non-target species resource selection. We used radio telemetry to determine how supplemental feeding of Northern Bobwhite (*Colinus virginianus*) may alter their resource selection and that of Timber rattlesnakes (*Crotalus horridus*) and Black rat snakes (*Pantherophis obsoletus*). We compared 2<sup>nd</sup> and 3<sup>rd</sup> order resource selection of each species between treatment areas with stocked supplemental feeders (“feeder-fed”) and empty feeders (“unfed”) or supplemental feedlines (“broadcast-fed”). The effects of food distribution were equivocal for Black rat snakes. Timber rattlesnakes and bobwhites occurred closer to supplemental feed when available, but bobwhites were more strongly affected by filled feeders than empty feeders or feedlines, and Timber rattlesnakes established their home ranges near feedlines than feeders. These results demonstrate that different distributions of food resources can affect both target prey and non-target predator behavior, unintentionally increasing spatial overlap between predator and prey species.

INDEX WORDS: Black Rat Snake, *Colinus virginianus*, *Crotalus horridus*, Home Range, Northern Bobwhite, *Pantherophis obsoletus*, Predator-prey Relationship, Random Walk, Resource Selection, Supplemental Feed, Timber Rattlesnake

EFFECT OF SUPPLEMENTAL FEEDING ON MOVEMENT AND SPACE USE OF  
PREDATOR AND PREY

by

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## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS .....	iv
LIST OF TABLES .....	vii
LIST OF FIGURES .....	ix
CHAPTER	
1 General Introduction .....	1
Literature Cited .....	3
2 Effect of Food Distribution on Timber Rattlesnake ( <i>Crotalus Horridus</i> ) and Black Rat Snake ( <i>Pantheropsis obsoleta</i> ) Resource Selection .....	6
Introduction.....	7
Methods.....	10
Results.....	20
Discussion .....	22
Literature Cited .....	27
3 Effect of Food Distribution on Resource Selection of Northern Bobwhite ( <i>Colinus virginianus</i> ) .....	48
Introduction.....	49
Methods.....	52
Results.....	59
Discussion .....	60

Literature Cited .....	63
4 Synthesis and Management Implications.....	83
APPENDECES .....	85
A Snake home range estimation and analysis.....	86
B Northern Bobwhite home range estimation and analysis .....	94



## LIST OF TABLES

	Page
Table 2.1: Covariates used in snake RSF analyses .....	33
Table 2.2: Summary of captured snakes .....	34
Table 2.3: Black rat snake random walk and 2 <sup>nd</sup> order RSF results study 1.....	35
Table 2.4: Black rat snake all 3 <sup>rd</sup> order RSF results study 1.....	36
Table 2.5: Black rat snake random walk and 2 <sup>nd</sup> order RSF results study 2.....	37
Table 2.6: Black rat snake all 3 <sup>rd</sup> order RSF results study 2.....	38
Table 2.7: Timber rattlesnake random walks and 2 <sup>nd</sup> order RSF results study 1 .....	39
Table 2.8: Timber rattlesnake all 3 <sup>rd</sup> order RSF results study 1 .....	40
Table 2.9: Timber rattlesnake random walks and 2 <sup>nd</sup> order RSF results study 2.....	41
Table 2.10: Timber rattlesnake all 3 <sup>rd</sup> order RSF results study 2 .....	42
Table 3.1: List of covariates used in Northern Bobwhite RSF analyses .....	69
Table 3.2: Northern Bobwhite 2 <sup>nd</sup> order RSF results study 1 .....	70
Table 3.3: Northern Bobwhite 3 <sup>rd</sup> order RSF results study 1 .....	71
Table 3.4: Northern Bobwhite 2 <sup>nd</sup> order RSF results study 2.....	73
Table 3.5: Northern Bobwhite 3 <sup>rd</sup> order RSF results study 2 .....	74
Table 3.6: Black rat snake home range analysis results.....	90
Table 3.7: Snake home range summaries between treatments .....	91
Table 3.8: Snake home range summaries between sexes .....	92
Table 3.9: Timber rattlesnake home range analysis results .....	93

Table 3.10: Northern bobwhite home range analysis results .....	98
Table 3.11: Northern Bobwhite home range summaries between treatments .....	99
Table 3.12: Northern Bobwhite home range summaries between sexes .....	100

## LIST OF FIGURES

	Page
Figure 2.1: Map of study area and treatments.....	43
Figure 2.2. Random walk and 2 <sup>nd</sup> order resource selection model predicted Black rat snake ( <i>Pantherophis obsoletus</i> ) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 .....	44
Figure 2.3. Random walk and 2 <sup>nd</sup> order resource selection model predicted Black rat snake ( <i>Pantherophis obsoletus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 2 in 2019 .....	45
Figure 2.4. Random walk and 2 <sup>nd</sup> order resource selection model predicted Timber rattlesnake ( <i>Crotalus horridus</i> ) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 .....	46
Figure 2.5. Random walk and 2 <sup>nd</sup> order resource selection model predicted Timber rattlesnake ( <i>Crotalus horridus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 2 in 2019 .....	47
Figure 3.1: Map of study area and treatments.....	76
Figure 3.2. 2 <sup>nd</sup> order resource selection model predicted Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.....	77

Figure 3.3. 3 <sup>rd</sup> order resource selection model Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 90% KUDs.....	78
Figure 3.4. 3 <sup>rd</sup> order resource selection model predicted Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 1 in 2018 within their 50% KUDs .....	79
Figure 3.5. 2 <sup>nd</sup> order resource selection model predicted Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 2 in 2019.....	80
Figure 3.6. 3 <sup>rd</sup> order resource selection model predicted Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 2 in 2019 within their 90% KUDs .....	81
Figure 3.7. 3 <sup>rd</sup> order resource selection model predicted Northern Bobwhite ( <i>Colinus virginianus</i> ) mean probability of use as a function of distance to feed in feeder and broadcast treatments during study 2 in 2019 within their 50% KUDs .....	82

## CHAPTER 1

### GENERAL INTRODUCTION

How resources are distributed across a landscape influences many ecological processes. For example, the distribution and movement patterns of both predator and prey are driven in large part by the distribution of food resources (Boyd, 1996; Sih, 1982), and this in turn contributes to the distribution of predation risk. Heterogenous dispersion of risk and resources can then affect risk-dependent behaviors by prey species. Prey must weigh predation risk against potential resources gained when selecting resource patches, and individuals may leave resource patches earlier when foraging in areas perceived to have high predation risk (Brown, 1992; Kotler, 1997). Prey are also expected to accept higher levels of risk while foraging if they are food deprived such as during times of resource scarcity or if they have high resource demands such as during juvenile growth or female production of eggs (Abrahams and Dill, 1989; Lima, 1998). In this way, changes in resource distribution can have effects across multiple trophic levels, and it is important to consider how management practices that alter the distribution of resources within a landscape for target species may also affect the distribution and behavior of nontarget competitors and predators.

Supplemental feeding is a common management action that artificially alters the distribution of certain food resources across a landscape. Although it is used to increase the survival or reproductive rates of target species (Hawkins, 1937; Townsend et al., 1999; Guthery et al., 2004), it has also been shown to concentrate predator distributions (Godbois et al., 2004; Turner et al., 2008). Predator responses may be the result of higher densities of nontarget prey

species around supplemental feed, and some worry that increased predator abundance or activity around supplemental feed may indirectly negatively impact the survival rate of the target, managed species (Doonan and Slade, 1995; Godbois et al., 2004; Guthery et al., 2004; Turner et al., 2008; Henson et al., 2012). A small number of studies have found no increase in predator-related mortalities of target species in supplementally fed areas (Townsend et al., 1999; Sisson et al., 2000); however, there have been no studies that directly, simultaneously estimate predator and prey behavioral responses to supplemental feeding and how that may alter the likelihood of interactions between target species and their predators or prey perception of risk.

There are different ways to distribute supplemental feed across a landscape, and different techniques may affect populations in unique ways. For example, stationary feeders attract foragers to small, localized, predictable areas. As a result, areas around feeders may be good hunting areas for predators compared to areas where supplemental feed is not provided or is evenly broadcast over larger areas. Broadcasting feed may be less likely to concentrate prey and increases the opportunity for individuals to forage while remaining in areas of preferred cover (Kassinis and Guthery, 1996; Buckley et al., 2015). Because different supplemental feeding approaches pose both predator and prey with different resource distributions, different approaches may result in different movement and space use patterns that could alter the potential for interactions.

Northern Bobwhite (*Colinus virginianus*) is a widely managed gamebird species for which supplemental feeding is a common component of management (Frye, 1954; Guthery, 1986). Timber rattlesnakes (*Crotalus horridus*) and Black rat snakes (*Pantherophis obsoletus*) follow chemical cues to areas their prey frequent in order to hunt and would likely benefit from hunting near supplemental feed (Clark, 2004; Degregorio et al., 2014). Their prey consists

primarily of small mammals (Fitch, 1963; Clark, 2002), which generally increase in areas of supplemental feeding (Doonan and Slade, 1995). While evidence suggests supplemental feeding may not directly negatively affect bobwhite survival (Townsend et al., 1999; Sisson et al., 2000), increased perceived risk may impact bobwhite behavior, resulting in sublethal effects that may impact fitness (Lima and Dill, 1990; Sheriff et al., 2009; Mohlman et al., 2019). Therefore, the objectives of this thesis were to determine whether supplemental feeding for bobwhite affects bobwhite, Timber rattlesnake, and Black rat snake resource use in a manner that might increase interactions between bobwhites and two predator species. This research will increase our understanding of how supplemental food resource distribution affects predator-prey interactions, may help explain the variable success of supplemental feeding to increase bobwhite populations.

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## CHAPTER 2

# EFFECT OF FOOD DISTRIBUTION ON TIMBER RATTLESNAKES (*CROTALUS HORRIDUS*) AND BLACK RAT SNAKES (*PANTHEROPHIS OBSOLETUS*) RESOURCE SELECTION<sup>1</sup>

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## ABSTRACT

It is important to understand the both the direct and indirect effects of management actions for target species. Supplemental feeding is a common management tool for game species that may influence space use and resource selection of their predators, which may in turn indirectly affect prey behavior and fitness. Timber rattlesnakes (*Crotalus horridus*) and Black rat snakes (*Pantherophis obsoletus*) are wide-ranging meso-predators that are likely to benefit from hunting near feed. We used radio-tracked movements within areas with stocked stationary bobwhite feeders (“feeder fed”) and non-supplementally fed (“unfed”; study 1, year 1) or non-stationary “broadcast-fed” (study 2, year 2) areas to compare resource selection within a Bayesian framework. The effects of food distribution were equivocal for Black rat snakes; however, Timber rattlesnakes were more likely to occur closer to supplemental feed when available and were more likely to establish their home ranges near feedlines than feeders. These results demonstrate that supplemental feed increases snake use of areas, though the effect can differ among species. Supplemental feeding increases the potential for overlap between non-target predator and target prey species, which may affect bobwhite survival or perceived risk and behavior in areas of supplemental feeding.

## INTRODUCTION

The distribution of prey influences the movement patterns and distribution of predators (Boyd, 1996; Sih, 1982). Consistent with optimal foraging theory, which suggests an animal should adopt the most energetically profitable foraging strategy (Kamil, 1983), predators often alter their behavior to decrease foraging time and more efficiently exploit resources patches by hunting in areas with higher prey densities (Stephens and Krebs 1986; Crabtree and Wolfe, 1988;

Lima and Dill, 1990; Sih, 1998). As a result, areas of high prey abundance often have high predator density (Vanni, 1987; Fedriani et al., 2001). However, the resulting dispersion of predators creates a heterogeneous distribution of risk, and the level of perceived risk within an area can then alter the behavior of prey (Brown, 1992; Kotler, 1997). By influencing prey choice of resource patches, predators play an important role in structuring ecosystems through both predation and the generation of fear (Brown, 1992; Kotler, 1997, Beschta and Ripple, 2009). Therefore, it is important to consider how management practices that may affect behavior of predators may then affect target species.

Supplemental feeding is a common management tactic that artificially alters the distribution of certain food resources across a landscape in an effort to increase the survival or reproduction of target species (Hawkins, 1937; Townsend et al., 1999; Godbois et al., 2004; Guthery et al., 2004; Turner et al., 2008); however, supplemental feed can increase the abundance of a variety of non-target species such as songbirds and rodents (Doonan and Slade, 1995; Guthery et al. 2004; Morris et al., 2011; Henson et al. 2012). Presumably as a result of this high concentration of prey, some predators appear more frequently near supplementally fed sites than expected (Godbois et al., 2004; Turner et al., 2008). Even when supplemental feeding does not increase predation on prey species (Townsend et al., 1999), increased prey perception of risk may alter prey behavior, resulting in sublethal reduction in fitness (Lima and Dill, 1990; Sheriff et al., 2009; Mohlman et al., 2019). Despite its potential importance in determining the effectiveness of supplemental feeding on target species, there are few studies that estimate the indirect, non-target effects of supplemental feeding on predator behavior.

Different methods of supplemental feed distribution may affect predators in unique ways. For example, stationary feeders attract prey to localized, fixed locations, which may result in

high local densities of prey species. Predators foraging in feeder-fed landscapes might then concentrate their foraging efforts near feeders. Alternatively, broadcasting feed over wider areas gives prey the opportunity to move and be more dispersed (Kassinis and Guthery, 1996; Buckley et al., 2015) Assuming prey would be less concentrated and their activity less predictable in broadcast feeding areas, predators hunting may be similarly less concentrated. Therefore, how supplemental feed is distributed may affect predator resource selection and the subsequent spatial distribution of risk to prey.

Timber rattlesnakes (*Crotalus horridus*) and Black rat snakes (*Elaphe obsoleta*) are examples of predators that might respond to supplemental feeding for game species in managed landscapes (Fitch 1963; Clark, 2002; Clark, 2004). Timber rattlesnakes are sit-and-wait ambush predators whose diet consists primarily of small mammals (Clark, 2002). They use chemical cues to find areas with high prey species diversity and abundance and can spend several days waiting in ambush in order to catch prey (Clark, 2002). The Black rat snake's diet is also mainly composed of small mammals (Degregorio et al., 2014), they routinely prey on small birds including eggs. Black rat snakes use chemical cues to actively trail their prey and, therefore, seem to forage opportunistically rather than spend long periods in areas of high prey abundance (Blouin-Demers and Weatherhead, 2001,a,b; Carfagno et al., 2006). Prior research indicates their preference for forest edges (i.e., within the 15 m boundary between forest and open habitat such as fields, marshes, roads) and their thermoregulatory behaviors are better predictors of rat snake movement and space use than is prey abundance (Blouin-Demers and Weatherhead, 2001,a,b; Carfagno et al., 2006; Sperry et al., 2009). Consequently, while both species may alter their resource selection in response to supplemental feeding, they might also differ in the magnitude or nature of their responses.

The objective of this study was to use radio-telemetry to determine how the presence of supplemental feed and method of distribution affected the resource selection of Timber rattlesnakes and Black rat snakes. We hypothesized that, because they are ambush foragers, would select areas closer to filled stationary feeders compared to either empty feeders or broadcast feedlines. We hypothesized that because Black rat snakes are more active searching predators and prior research shows strong selection to structural habitat features (Blouin-Demers and Weatherhead, 2001,a,b; Carfagno et al., 2006; Sperry et al., 2009), they would be more likely to select for supplementally fed areas nearer to forest edges. More specifically, given broadcast feeding distributes feed over more area near or within forest edge than stationary feeders, we predicted the probability a Black rat snake would select for areas near feed would be greater near feedlines than near feeders.

## METHODS

### *Study Area*

Di-Lane Wildlife Management Area encompasses 3,359 ha of federally owned land located in the Upper Coastal Plains of Burke County, Georgia. Di-Lane is managed by the Georgia Department of Natural Resources (DNR) to promote the growth of early successional habitat with a management emphasis on Northern Bobwhite (*Colinus virginianus*). Techniques such as disking, timber thinning, prescribed burning, and herbicide application are used to maintain a mixture of fallow fields [mostly camphorweed (*Heterotheca subaxillaris*), common ragweed (*Ambrosia artemisiifolia*), partridge pea (*Chamaecrista fasciculata*), annual low panic grasses (*Dichanthelium* spp.; perennial broomsedge, *Andropogon virginicus*; and split-beard bluestem, *Andropogon ternarius*)], loblolly pine uplands (*Pinus taeda*), hardwoods [mostly oaks, *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 pine uplands were burned and the fallow fields disked on a 2-3 year rotation. In addition, biannual meso-mammal predator control and year-round supplemental feeding using sorghum (*Sorghum bicolor*) were used to increase bobwhite survival. Average temperatures for Burke County, Georgia range from 31.6 to 15 °C for the month of May and 33.3 to 19.4 °C in June through August with little variation between months. Average rainfall is approximately 6.4 cm in May and ranges from 12.6 to 13.4 cm in June through August (National Climate Data Center, National Oceanic and Atmospheric Administration).

### *Experimental Design*

Beginning in 2008, stationary feeders were the sole method of supplemental feed distribution before our study took place. A total of 223 feeders were placed within the study area of a mean density of 7 feeders per ha<sup>2</sup>. The average distance between feeders was 175 m. Ninety seven percent of feeders were located within patches of scrub shrub with medium to high density vegetative cover on all sides. Those not in scrub shrub were within the edges of tree lines with comparatively little adjacent cover. Feeders were sometimes placed near roads, which Timber rattlesnakes will sometimes avoid (Steen et al., 2012); however, there were no other features scrub shrub and roads that would have likely affected snake use of fed sites. All supplemental feed operations were carried out by the Georgia DNR.

#### *Study 1: Fed vs. Unfed Experiment*

In 2018, we split Di-Lane into eastern and western units (1501 ha and 1342 ha, respectively) and randomly assigned the eastern unit as a feeder-fed treatment and the western unit initially as an unfed treatment (Figure 2.1). Beginning June 12th, 2018, all feeders on the

eastern half of the property ( $n = 131$ ) were filled with sorghum and all feeders on the western half ( $n = 92$ ) were emptied of any remaining sorghum and left in place to create the unfed treatment. Ten random feeders within the feeder-fed treatment were checked each week to monitor fill level.

### *Study 2: Feeder Fed vs. Broadcast Fed Experiment*

In 2019, the eastern treatment area remained as a feeder-fed treatment, and the western treatment area became the broadcast-fed treatment (Figure 2.1). Ten random feeders within the feeder-fed treatment were checked every week and were refilled when necessary. Beginning May 20<sup>th</sup>, 2019, sorghum was broadcast along a predetermined route within the western half of the property. Feed lines were mapped along pre-existing roads and firebreaks (spaced 100 – 300 m apart). The total feed route was approximately 63 km long at an average density of 3.25 km per 100 ha<sup>2</sup>. Feed was spread at a rate of 5.38 bushels/ha/yr at an average width of 13 m. Broadcast feeding occurred once every two weeks as described by Buckley et al. (2015).

Before the broadcast feeding treatment was put in place, feeders within the treatment were full during turkey hunting season (March 21<sup>st</sup> - May 15<sup>th</sup> of 2019) to continue supplemental feeding of bobwhite while complying with Georgia law prohibiting turkey hunting over bait. Nearly all feeders within the broadcast treatment were emptied within one week following turkey season; however, in early July, we found 11 feeders were still filled with seed. Upon discovery, sorghum was removed from the feeders, and all other feeders within the treatment were checked and verified to be empty.

### *Snake Trapping and Processing and Implantation of Radios*

The majority of the Timber rattlesnakes ( $n = 21$ ) and Black rat snakes ( $n = 27$ ) included in our study were found opportunistically on roads and firebreaks and were hand-captured



between April and June of both study years. Eleven more snakes (5 Timber rattlesnakes, 6 Black rat snakes) were captured in or around Stoddard funnel traps that were distributed evenly across the study site and had been set for bobwhite in October of 2018 as a part of another study. All captured snakes were subcutaneously implanted with a Passive Integrated Transponder (PIT) tag measuring either 9 mm or 23 mm, depending on the size of the snake. Captured snakes were also weighed to the nearest 1 g and snout-vent-length (SVL) measured to the nearest 0.1 cm. Radio-transmitters (Advanced Telemetry Systems 4g model series R1100 or 13g model series M1200, depending on size of the animal; Advanced Telemetry Systems, Inc., Isanti, MN, U.S.) were surgically implanted within snakes by a veterinarian following the methods outlined in Reinert and Cundall (1982). All transmitters weighed less than 3% of snake's mass. Snakes were treated with analgesics and held for three days post-surgery to monitor for signs of infection. Snakes were treated with a final dose of antibiotics before release at their original capture location (GA collection permit: 1000602439; IACUC AUP: A2017 10-003-Y3-A3). Because gravid females of both species move significantly less and occupy significantly different habitat than nongravid females (Reinert and Zapporlorti, 1988; Blouin-demers and Weatherhead 2001a,b), gravid females were not implanted with transmitters. Juvenile Black rat snakes were also not included in the study.

### *Radio Telemetry of Snakes*

Beginning the day after release, snakes were relocated a minimum of once per day for 6 days each week using Biotracker receivers and 3-element directional antennae from Lotek Wireless Inc. (Newmarket, ON, Canada) via homing telemetry (White and Garrott, 1990; Amelon et al., 2009). We divided the 24 hour day into 5 equal time slots and used a random number generator to assign each tracking day a time slot without replacement until all time slots

were represented within a week before we randomly assigned the 6<sup>th</sup> tracking day a time slot. Relocations occurred at varying times of day and night throughout each week to account for potential differences between diurnal and nocturnal activity. Global positioning systems (GPS) were used to obtain observer locations, and compasses were used to determine the azimuth to the snake. Ambient temperature and sky condition (United States Weather Service sky condition scale) were recorded with every relocation. Approximate locations were taken 20 - 30 m from the snakes to minimize disturbance. All snakes remaining at the end of the first active season were tracked twice per week until the next active season began to minimize loss of snakes during winter.

### *Statistical Analyses*

To ensure analyses only included data collected when supplemental feed was being reliably distributed within the designated treatments, only data gathered between dates June 12<sup>th</sup>, 2018 – Sept 1<sup>st</sup>, 2018 and May 20<sup>th</sup>, 2019 – Sept 7<sup>th</sup>, 2019 were used in analyses. Snakes did not travel to other designated feeding treatments outside of their assigned treatment throughout the duration of the experiment. Data collected for each species within each year were analyzed separately for ease of interpretation.

All analyses were conducted within a Bayesian framework using R (R Core Team, 2019) and R package jagsUI (Kellner, 2019), and 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 iteration, adaptation, and burn-in values with a thinning rate of 10 in order 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 below 1.1

(Gelman et al., 2004). Values of all estimated parameters had an R-hat value of 1.1 or below, and visual inspection of trace plots further confirmed chain convergence. We reported posterior means and 95% and 50% credible intervals for parameters of interest. We also reported Bayesian *P*-values by calculating the proportion of the posterior distribution with the same sign as the mean to estimate the maximum probability of effect (Makowski et al., 2019). We used iterations and burn-in values of adequate number to characterize the posterior distributions, ensure MCMC chains showed no indications of autocorrelation or effects of initial values, and ensure that all chains converged. 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 -.05 to .05. If there is partial overlap between the ROPE and posterior distribution, it is uncertain whether the effect was significant (Kruschke, 2014). Generally, only effects in which >97.5% of the posterior distribution did not overlap the ROPE were mentioned in our results.

### *Land Cover Analysis*

Land cover data was gathered using 10 m resolution Sentinel-2 imagery data generated by the European Space Agency (ESA) in 2018 and provided by the United States Geological Survey (USGS). We conducted supervised classification in ArcGIS (ESRI 2019) by generating training polygons of the desired land cover types (e.g., forest and scrub shrub) within Sentinel-2 imagery and creating a confusion matrix to determine map accuracy. The confusion matrix was made up of 500 random points distributed via stratified random sampling across landcover types of interest and ground-truthed for accuracy. We determined map accuracy to be 90.77% for forest and 73.26% for scrub shrub vegetation. Similar to Blouin-Demers and Weatherhead (2001 a,b), we considered our study species to be in a forest edge when they were within 20 m of the

boundary between any forest and non-forest land cover. Scrub shrub was an average of 26 m from any random point within the study area while forest edge was an average of 21.5 m from any random point.

### *Resource Selection Function Analyses*

#### *Traditional Home Range RSF Approach*

To estimate study species' selection of scrub shrub, forest edge, and supplementally fed areas, we used a resource selection function (RSF) to analyze the distance of each telemetry relocation (used) as well as randomly generated locations (available) to the closest feature of each resource type (Manly et al., 2002). We modeled RSFs at 2<sup>nd</sup> (i.e., selection of home ranges within the landscape) and 3<sup>rd</sup> order (i.e., selection of resources within each home range) scales as described by Johnson (1980). Adequate coverage of an area is important when considering how many available locations to generate within each boundary of interest (Buskirk and Millsaugh, 2006), and using the same number of available points to sample each home range may not equally sample all home ranges. As a result, we chose to incorporate the 5:1 ratio of available:used points used in discrete choice modeling as outlined by Cooper and Millsaugh, (1999; 2001) to sample relevant areas.

Home ranges were estimated to determine availability at the 3<sup>rd</sup> order selection scale (Appendix A), and random locations ("available") were generated within each snakes' home range equal to five times the number of telemetry relocations ("used") recorded for each individual. For 2<sup>nd</sup> order selection, we created a minimum bounding polygon surrounding all used locations of all snakes of each species within each treatment area using the Minimum Bounding Geometry tool in ArcGIS (ESRI 2019) and buffered them by their average daily movement distance.

### *Random Walk RSF Approach*

A limitation of traditional RSF models is that available locations are bound to the minimum area where animals were observed bounded arbitrarily by average daily movement. This precludes sampling of some available habitats with the movement capabilities of animals. “Random walks” simulated from actual animal movements create an alternative means to sample areas beyond the minimum area of observed locations. Random walks incorporate observed movement distances (step lengths) and trajectories to create random movement tracks unconstrained by home range boundaries. As an added benefit, individuals without the minimum number of relocations necessary for a home range to reach equilibrium can still be included in analyses. Consequently, traditional RSFs and random walk RSFs are fundamentally different in how they sample random space and parameter effects found to be similar between the two approaches are likely to be more robust rather than dependent on how available points are randomly sampled. Since snake home range estimates in this study did not reach a stable equilibrium as assumed by a traditional RSF (Appendix A; Johnson, 1980), we chose to compare traditional 2<sup>nd</sup> order selection and random walk RSF results to make inferences about factors affecting snake habitat use.

We again utilized a 5:1 ratio of available: used points and used a random walk model to simulate 5 randomly moving snakes per radio-telemetered snake to generate available locations. Each set of 5 random walks began at the first telemetry location of the telemetered snake they were paired with, and each walk was generated with the same number of relocations collected for that individual. To ensure simulated snakes traveled similar distances and made similar movements between consecutive locations as our study animals,

we incorporated step length and turning angles of radio-telemetered individuals into the random walk model.

Step lengths and turning angles were calculated using R package “moveHMM” (Michelot et al., 2019). To standardize time between successive relocations, we interpolated one location per day of missing telemetry data using R package “imputeTS” (Mortiz and Bartz-Beielstein, 2017) when greater than one calendar day passed between relocations. Step length and turning angle values were excluded from the random walk model when telemetry data was unavailable for four or more days between successive relocations. Only step lengths of relocations >12 hours apart were used to calculate the step length distribution to reduce spatial autocorrelation. Step lengths <5 m were made to equal zero to account for telemetry and GPS error. In addition, separate distributions of male and female step lengths and turning angles of each species were used to generate those of simulated snakes (Durner and Gates, 1993; Blouin-demers et al., 2007; MacGowan et al., 2016; Petersen et al., 2019), where the distribution used to generate random walks was based on the sex and species of the individual the walks were paired with.

### *RSF Modeling*

For both the traditional and random walk approaches, we calculated the Euclidean distance to the closest feature of each resource type (forest edge and feeder or feedline depending on treatment) of all used and available locations using the Generate Near Table tool in ArcGIS (ESRI 2019). Distance to feeders as well as distance to feedline of Black rat snakes in the broadcast-fed treatment were calculated to account for exposure to the overlooked feeders in later analyses.

We constructed separate logit models with random intercepts within a Bayesian framework for each species in each year to estimate resource selection relative to resource availability. Models included random intercepts to properly account for the variation caused by the dependent nature of successive telemetry locations as well as the individual variation in their response to treatment effects (Gillies et al., 2006; Coppes et al., 2018). Although random slopes can be included to further account for individual variation in treatment effects (Gillies et al., 2006), presumably due to our sample size, we were unable to obtain model convergence when we incorporated both random slopes and random intercepts.

We assigned normal distributions to random effects with a mean of 0 and with vague gamma-distributed precision terms (1/variance). We used vague normal priors for fixed effects (mean = 0, precision = 0.001). Distance related numerical predictors were divided by 10 to make a more meaningful output. Non-distance 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:

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

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

$$\beta_{0,j} \sim \text{Norm}(\mu, \tau);$$

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

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

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,  $k = 1, 2, \dots$  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 2.1.

## RESULTS

Our traditional RSF analyses exclude individuals without enough relocations to estimate a home range while our random walk RSF incorporated all individuals. As a result, sample size differs between analyses (Table 2.2). In addition, scrub shrub was well dispersed throughout our study site, and 87% of 2279 total observed Black rat snake locations and 85% of 1379 total observed Timber rattlesnake observations occurred within 20 m of scrub shrub. As a result, distance to scrub shrub was uninformative and not included in our models.

### *Black Rat Resource Selection*

#### *Study 1: Feeder-fed Treatment vs Unfed Treatment*

When using the random walk and 2<sup>nd</sup> order approaches, distance to feeder had a small effect on probability of resource use, where for every 10 m increase in distance to feeder, probability of use decreased by 4% and 5%, respectively, regardless of treatment (Table 2.3, Figure 2.2). However, ROPE values indicated the effect of feed was negligible when using the random walk approach, and the effect was small and potentially negligible when using the 2<sup>nd</sup> order approach. When using the random walk approach, for every 10 m increase in distance to forest edge, probability of resource use decreased by 8% (Table 2.3), but we did not find a similar trend when using the 2<sup>nd</sup> order approach (Table 2.3). For 3<sup>rd</sup> order models within both 90% and 50% isopleths, Black rat snake selection for areas near feeders was negligible in both treatments (Table 2.4).



### *Study 2: Feeder-fed treatment vs Broadcast-fed treatment*

When using the random walk approach, while individuals within the feeder-fed treatment were more likely to be closer to feed than those in the broadcast-fed treatment, ROPE values indicated both the estimated effect of distance to feed and the interaction between distance to feed and treatment was negligible (Table 2.3, Figure 2.3). When using the 2<sup>nd</sup> order approach, Black rat snakes in the broadcast-fed treatment were somewhat closer to feed than snakes in the feeder-fed treatment (Table 2.3, Figure 2.3); however, the effect size was small and potentially negligible according to our ROPE values, and the effect of the interaction between distance to feed and treatment estimated by the random walk model was opposite that of the effect estimated by the 2<sup>nd</sup> order model. The random walk model did estimate a somewhat small positive effect of distance to forest edge on probability of Black rat snake use; however, the 2<sup>nd</sup> order model estimated a negative effect of distance to forest edge on probability of use (Table 2.5). Based on the random walk model, for every 10 m increase in distance to forest edge, probability of resource use decreased by 5% whereas probability of use increased by 6% when using the 2<sup>nd</sup> order approach (Table 2.5). Effect sizes of all main effects and interaction terms were either minor or were unlikely to have influenced probability of resource use within the 3<sup>rd</sup> order scale (Table 2.6).

### *Timber Rattlesnake Resource Selection*

#### *Study 1: Feeder-fed Treatment vs Unfed Treatment*

Based on the random walk and 2<sup>nd</sup> order approaches, Timber rattlesnake probability of use increased with increasing proximity to feeders regardless of treatment (Table 2.7), where for every 10 m increase in distance to feeder, probability of use increased by 8% or 6% respectively (Figure 2.4). The random walk and 2<sup>nd</sup> order approaches also estimated effects of the distance to

forest edge, where for every 10 m increase in distance from forest edge, probability of use decreased by 15% and 9%, respectively (Table 2.7). Unlike the prior models, there was little to no effect of distance to feed in the 3<sup>rd</sup> order models of home ranges (Table 2.8). For every 10 m increase in distance of Timber rattlesnakes to forest edge, probability of use decreased by 10% based on the 90% core use model (Table 2.8).

#### *Study 2: Feeder-fed treatment vs Broadcast-fed treatment*

Based on the random walk and 2<sup>nd</sup> order model estimates, distance to feed had a small effect on probability of use by Timber rattlesnakes, where individuals were somewhat more likely to use areas closer to feedlines in the broadcast-fed treatment than to feeders in the feeder-fed treatment (Table 2.9, Figure 2.5). For every 10 m increase in distance to forest edge, the random walk model estimated Timber rattlesnake probability of use increased by 14% (Table 2.9). The effect of forest edge was negligible when using the 2<sup>nd</sup> order approach (Table 2.9). The 3<sup>rd</sup> order core area models for Timber rattlesnake detected negligible effects of treatments or covariates. The effect of distance to feed and the interaction between distance to feed and treatment were muted in both 3<sup>rd</sup> order models (Table 2.10).

## **DISCUSSION**

We explored the hypothesis that food distribution would differentially affect resource use for two species of snakes with different foraging behaviors and whether other resources such as forest edge would affect probability of use, particularly for Black rat snakes. Results from our two experiments and models were equivocal regarding the effect of distance to feed and treatment on probability of use, and it appears that any effect of supplemental feed was likely negligible. We also found no consistent evidence that Black rat snakes selected for areas near forest edge despite regular observation of Black rat snakes in trees (personal obs.) and other

research showing Black rat snakes preferred forest edge (Durner and Gates, 1993; Blouin-Demers and Weatherhead, 2001a,b). As a result, we were unable to reject the null hypothesis that distance to supplemental feed and its distribution in relation to forest edge did not impact Black rat snake resource selection. It is possible that any effect of supplemental feeding or other factors depends on factors we did not identify or that vary from year to year. A key assumption of our study is that supplemental feed increased prey availability for rat snakes, it did so similarly between years for stationary feeders and among all supplemental feed locations, and rat snakes could perceive this change through some mechanism. We were unable to measure prey availability, so we cannot evaluate this assumption. If the effects of supplemental feeding on other prey taxa are temporally or spatially variable, this may have obscured our ability to measure supplemental feeding effects on snake behavior.

Timber rattlesnakes selected for areas closer to feeders at a broader (2<sup>nd</sup> order/random walk) scale regardless of treatment but not at the local scale (3<sup>rd</sup> order). In other words, Timber rattlesnakes were more likely to establish their home ranges near feed but not more likely to use areas closer to feed within their home ranges. The increased likelihood of selecting home ranges near feed was stronger in the broadcast fed treatment compared to the stationary feeder treatment. At the broader scale, it is unclear why individuals within the unfed treatment in 2018 were more likely to use areas proximate to feeders even though the feeders were empty. Snakes were opportunistically caught regardless of their distance to feeders, so initial capture locations were unlikely to have caused this effect. Given that feeders were full prior to the start of our study in 2018, it is possible this reflects a legacy of prior experience with greater foraging success near feeders. Timber rattlesnakes will show fidelity to foraging areas and learn from past foraging experiences (Clark, 2004). Timber rattlesnakes also exhibit home range fidelity from

year to year (Reinert and Zappalorti, 1988). Individuals may have established home ranges nearer to feeders prior to 2018 and may have continued to visit areas near empty feeders as a result of past foraging successes in that area. In addition, our estimates of Timber rattlesnake home ranges never reached an asymptote. The failure to identify effects of distance to feeder within individual home ranges may be related to either the extent to which a supplemental feeder affects the distribution of prey at a more local scale and the local importance of cover. Timber rattlesnakes sometimes strongly selected for areas closer to forest edge on the landscape scale and within their 90% home ranges, suggesting high importance of this habitat type for use. Therefore, Timber rattlesnakes may benefit from increased prey density in the area even if they do not forage directly at feeders and choose area of forest edge for protection within areas close to supplemental feed. However, we note that in 2019, the pattern was not as strong and was only observed when using the random walk method. This illustrates the difficulty of making generalities about the importance of factors influencing snake habitat use, particularly from one or a few studies and over relatively short time scales for a long-lived animal. It may also indicate that commensurate activities common to landscapes managed for wildlife such as timber harvests may alter how factors affect the space use of predators and their potential for interactions with prey species.

We found general support for our hypothesis that supplemental feed distribution indirectly affect Timber rattlesnake resource selection; however, our results contradicted our predictions about the relative effect of stationary feeders vs broadcast feedlines. While Timber rattlesnakes increased use of areas near supplemental feed at the broader scale, we found that proximity to feed increased in the area of broadcast feeding compared to stationary feeding. In hindsight, our hypothesis was overly simplistic. First, broadcasting feed along feedlines

distributed more feed over a wider area. So, there is likely more supplemental feed in the broadcast treatment, which may create larger areas of high prey abundance that are attractive areas for rattlesnakes to establish home ranges.

Our Timber rattlesnake findings differ from a study by Nowak et al. (2015) that found the Western diamondback (*Crotalus atrox*) only had a weak response to the presence of supplemental feeders within their foraging ranges and seasonal migration routes (Nowak et al., 2015). However, Nowak et al. (2015) installed new, small, closely packed groups of feeders in two relatively small areas. In contrast, our study used larger areas with longer histories of supplemental feeding. Therefore, snakes in our study were, presumably, more likely to come across feed areas and likely had prior knowledge of feeder locations as well as of the comparative foraging quality of resource patches within the area. Consequently, the scale and duration of supplemental feed distribution may be an important factor in how the presence of feeders indirectly impacts the resource selection of predators that are slower to adapt to a newly modified landscape.

Taken collectively, our results imply that supplemental feed may concentrate the foraging efforts of Timber rattlesnakes, but not necessarily Black rat snakes, in areas close to supplemental feed. In addition, methods of food distribution may uniquely impact the resource selection of Timber rattlesnakes. While Timber rattlesnakes were likely to select for areas near feed regardless of distribution method, they were more likely to establish their home ranges closer to feedlines. We note that the strength of these effects was not consistent among models or years [within the stationary feed treatment], indicating the importance of using multiple modeling approaches to draw inferences and the need for integrating other potential factors and larger and longer studies with more sampling that can accommodate more complex and intensive models.

As Black rat snakes are quail nest predators (Fies and Puckett, 2000), their apparent lack of selection for feed sites may be good news for land managers employing supplemental feed for the purpose of increasing quail survival. However, it is possible we did not consider Black rat snake selection at a large enough scale to notice a trend. For example, birds and their eggs are a large component of a Black rat snake's diet during the summer months (Fitch, 1963). Songbirds that utilize supplemental feed will continue to nest in forests regardless of the location of the feed, and Black rat snakes exploiting songbirds and their nests would not need to forage directly at feeders or feedlines to profit. Conversely, Timber rattlesnakes, whose diet contains a higher percentage of small mammals than Black rat snakes (Fitch, 1963; Clark, 2002), may be more likely to have needed to forage near supplemental feed to exploit populations of small mammals utilizing the feed. As a result, future research investigating the effect of supplemental feed on Black rat snake resource selection may benefit from comparing individual selection on a larger scale.

Our research also implies that predators may select for areas near feeders months after feed was no longer being distributed, suggesting managers may benefit from periodically altering the location of feeders and feedlines to keep predators from getting habituated to hunting in specific locations. We were unable to determine how each method of supplemental feeding affected prey abundance, and future researchers looking to replicate our results should estimate prey abundance in order to make stronger conclusions and forego making assumptions based off previous literature. In addition, using different types of feed such as milo or corn may affect prey populations differently and thus may affect predator responses, and future research should focus on how using different feed types may have more severe consequences on predator resource selection than others. A next phase in this research is to determine whether the effects of

supplemental feeding on probability of snake use is sufficient to create meaningful risk for bobwhite quail or other managed species. Supplemental feeding may increase the overall abundance of snake species, creating an overall greater risk of target species mortality. As long as this additional mortality does not exceed the benefits of target species fitness, indirect supplemental feeding effects on snakes may not be a problem for managed species populations. Alternatively, while Timber rattlesnakes are not normally considered significant predators of quail, supplemental feed may draw quail and Timber rattlesnakes into more frequent contact and increase the relevance of Timber rattlesnakes as predators. An additional application of this research with regards to rattlesnakes is how it can inform our understanding of the likelihood snakes will encounter humans. Encounters between technicians filling supplemental feeders and snakes is likely to increase the killing of snakes, which would counter the indirect management benefit these species receive from game management.

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## TABLES AND FIGURES

Table 2.1. Description of covariates used in RSF analyses in years 2018 and 2019.

<b>Covariate</b>	<b>Description</b>
Edge	Distance to forest edge (m)
Treatment	Feeding treatment
Feed	Distance to nearest feeder or feedline depending on treatment (m)
Feed * Treatment	Interaction between distance to nearest fed area and treatment
Feed * Edge	Interaction between distance to nearest fed area and distance to forest edge
Feed * Edge *	Interaction between distance to nearest fed area, distance to forest edge, and
Treatment	treatment

Table 2.2. Summary of the number (*n*) of Timber rattlesnakes (*Crotalus horridus*) and Black rat snakes (*Pantherophis obsoletus*) used in traditional RSF analyses (Trad) and random walk RSF analyses (RW).

Species	Year	Sex	SVL Lower (cm)	SVL Upper (cm)	Treatment	n (RW)	n (Trad)
Timber Rattlesnakes	2018	M	97	126	Unfed	3	3
					Feeder Fed	6	6
		F	62.5	119	Unfed	3	3
					Feeder Fed	2	2
	2019	M	98.5	119	Broadcast Fed	5	4
					Feeder Fed	4	3
		F	67.5	129.5	Broadcast Fed	2	0
					Feeder Fed	1	0
Black Rat Snakes	2018	M	101.5	174	Unfed	8	7
					Feeder Fed	4	1
		F	107	138	Unfed	2	2
					Feeder Fed	3	2
	2019	M	101.5	159.5	Broadcast Fed	10	8
					Feeder Fed	3	3
		F	103	148	Broadcast Fed	4	2
					Feeder Fed	5	4

Table 2.3. Logistic regression results and credible intervals for Black rat snake (*Pantherophis obsoletus*) random walks and 2<sup>nd</sup> order resource selection functions for study 1 in year 2018. Intercept denotes the effect of the unfed treatment on females.

Method	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Random Walk	Intercept	-1.03	-0.89	-0.81	-0.73	-0.58	1.00	-
	Edge	-0.13	-0.10	-0.08	-0.07	-0.03	1.00	5.15
	Treatment	0.15	0.38	0.51	0.64	0.88	1.00	-
	Feed	-0.05	-0.04	-0.04	-0.04	-0.03	1.00	100.00
	Feed * Treatment	-0.05	-0.03	-0.03	-0.02	-0.01	1.00	100.00
	Feed * Edge	-0.01	-0.01	0.00	0.00	0.00	0.98	100.00
	Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.84	100.00
Traditional 2nd Order	Intercept	-0.85	-0.69	-0.61	-0.53	-0.37	1.00	-
	Edge	-0.06	-0.01	0.02	0.04	0.09	0.66	87.46
	Treatment	-0.16	0.14	0.30	0.46	0.76	0.89	-
	Feed	-0.06	-0.06	-0.05	-0.05	-0.04	1.00	37.60
	Feed * Treatment	-0.04	-0.02	-0.01	0.00	0.02	0.77	100.00
	Feed * Edge	-0.02	-0.02	-0.01	-0.01	-0.01	1.00	100.00
	Feed * Edge * Treatment	-0.03	-0.02	-0.02	-0.01	-0.01	1.00	100.00

Table 2.4. Logistic regression results and credible intervals for Black rat snake (*Pantherophis obsoletus*) 3<sup>rd</sup> order resource selection in relation to feeder-fed and unfed treatments in study 1 in year 2018. Intercept denotes the effect of the unfed treatment on females.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.72	-1.52	-1.42	-1.32	-1.12	1.00	-
	Edge	-0.05	0.00	0.03	0.05	0.10	0.75	75.78
	Treatment	-0.39	-0.05	0.15	0.33	0.69	0.70	-
	Feed	-0.02	-0.01	-0.01	0.00	0.01	0.76	100.00
	Feed * Treatment	-0.03	-0.01	0.00	0.01	0.03	0.51	100.00
	Feed * Edge	-0.02	-0.02	-0.01	-0.01	0.00	1.00	100.00
	Feed * Edge * Treatment	-0.03	-0.02	-0.02	-0.01	0.00	0.99	100.00
50%	Intercept	-1.99	-1.73	-1.60	-1.48	-1.24	1.00	-
	Edge	-0.07	0.00	0.03	0.06	0.12	0.72	68.54
	Treatment	-0.53	-0.12	0.10	0.32	0.78	0.62	-
	Feed	-0.02	0.00	0.01	0.01	0.03	0.68	100.00
	Feed * Treatment	-0.07	-0.04	-0.02	-0.01	0.02	0.83	95.46
	Feed * Edge	-0.03	-0.02	-0.01	-0.01	0.00	0.99	100.00
	Feed * Edge * Treatment	-0.01	0.00	0.01	0.02	0.03	0.86	100.00



Table 2.5. Logistic regression results and credible intervals for Black rat snake (*Pantherophis obsoletus*) random walk and 2<sup>nd</sup> order resource selection in study 2 in year 2019. Intercept denotes the effect of the broadcast-fed treatment on females.

Method	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Random Walk	Intercept	-1.28	-1.18	-1.13	-1.08	-0.97	1.00	-
	Edge	-0.09	-0.07	-0.05	-0.04	-0.02	1.00	41.24
	Treatment	0.43	0.61	0.71	0.80	1.00	1.00	-
	Feed	-0.04	-0.04	-0.03	-0.03	-0.02	1.00	100.00
	Feed * Treatment	-0.03	-0.02	-0.02	-0.01	0.00	1.00	100.00
	Feed * Edge	-0.02	-0.02	-0.02	-0.02	-0.01	1.00	100.00
	Feed * Edge * Treatment	0.01	0.01	0.01	0.01	0.02	1.00	100.00
Traditional 2nd Order	Intercept	-1.34	-1.24	-1.19	-1.13	-1.03	1.00	-
	Edge	0.01	0.04	0.06	0.08	0.11	0.99	33.51
	Treatment	-0.94	-0.76	-0.66	-0.57	-0.39	1.00	-
	Feed	-0.04	-0.03	-0.03	-0.02	-0.02	1.00	100.00
	Feed * Treatment	0.04	0.05	0.05	0.06	0.07	1.00	30.87
	Feed * Edge	-0.06	-0.05	-0.04	-0.04	-0.03	1.00	83.04
	Feed * Edge * Treatment	0.02	0.03	0.03	0.04	0.05	1.00	100.00

Table 2.6. Logistic regression results and credible intervals for Black rat snake (*Pantherophis obsoletus*) 3<sup>rd</sup> 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.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.66	-1.55	-1.49	-1.43	-1.32	1.00	-
	Edge	-0.07	-0.03	-0.01	0.01	0.04	0.66	97.51
	Treatment	-0.25	-0.05	0.06	0.18	0.39	0.66	-
	Feed	-0.02	0.00	0.00	0.01	0.02	0.53	100.00
	Feed * Treatment	-0.02	-0.01	0.00	0.00	0.02	0.59	100.00
	Feed * Edge	-0.04	-0.03	-0.03	-0.02	-0.02	1.00	100.00
	Feed * Edge * Treatment	0.01	0.02	0.02	0.03	0.03	1.00	100.00
50%	Intercept	-1.76	-1.63	-1.56	-1.50	-1.37	1.00	-
	Edge	-0.09	-0.04	-0.02	0.01	0.05	0.68	87.06
	Treatment	-0.47	-0.20	-0.07	0.06	0.31	0.64	-
	Feed	-0.01	0.00	0.01	0.01	0.03	0.75	100.00
	Feed * Treatment	-0.03	-0.01	0.00	0.01	0.03	0.52	100.00
	Feed * Edge	-0.05	-0.03	-0.03	-0.02	-0.01	1.00	100.00
	Feed * Edge * Treatment	0.01	0.02	0.02	0.03	0.04	1.00	100.00

Table 2.7. Logistic regression results and credible intervals for Timber rattlesnake (*Crotalus horridus*) random walk and 2<sup>nd</sup> order resource selection functions for study 1 in year 2018. Intercept denotes the effect of the unfed treatment on females.

Method	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Random Walk	Intercept	-0.82	-0.58	-0.47	-0.34	-0.09	0.99	-
	Edge	-0.18	-0.16	-0.14	-0.13	-0.10	1.00	0.00
	Treatment	0.15	0.46	0.62	0.77	1.09	1.00	-
	Feed	-0.09	-0.08	-0.08	-0.07	-0.06	1.00	0.00
	Feed * Treatment	-0.08	-0.07	-0.06	-0.05	-0.03	1.00	24.13
	Feed * Edge	0.01	0.01	0.01	0.01	0.01	1.00	100.00
	Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.99	100.00
Traditional 2nd Order	Intercept	-0.93	-0.75	-0.65	-0.56	-0.38	1.00	-
	Edge	-0.13	-0.10	-0.09	-0.07	-0.04	1.00	0.00
	Treatment	-0.13	0.11	0.23	0.36	0.61	0.90	-
	Feed	-0.07	-0.06	-0.06	-0.05	-0.05	1.00	3.62
	Feed * Treatment	-0.07	-0.06	-0.05	-0.04	-0.03	1.00	57.16
	Feed * Edge	0.00	0.00	0.00	0.00	0.01	1.00	100.00
	Feed * Edge * Treatment	0.00	0.01	0.01	0.01	0.01	1.00	100.00

Table 2.8. Logistic regression results and credible intervals for Timber rattlesnake (*Crotalus horridus*) 3<sup>rd</sup> order resource selection in relation to feeder-fed and unfed treatments in study 1 in year 2018. Intercept denotes the effect of the unfed treatment on females.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.53	-1.33	-1.23	-1.13	-0.93	1.00	-
	Edge	-0.16	-0.12	-0.10	-0.09	-0.05	1.00	0.00
	Treatment	-0.03	0.26	0.40	0.54	0.80	0.97	-
	Feed	-0.04	-0.03	-0.03	-0.02	-0.01	1.00	100.00
	Feed * Treatment	-0.06	-0.05	-0.04	-0.03	-0.01	1.00	85.87
	Feed * Edge	0.00	0.00	0.00	0.00	0.00	1.00	100.00
	Feed * Edge * Treatment	0.00	0.00	0.01	0.01	0.01	1.00	100.00
50%	Intercept	-1.84	-1.61	-1.49	-1.38	-1.17	1.00	-
	Edge	-0.09	-0.05	-0.03	-0.01	0.04	0.80	77.13
	Treatment	-0.30	0.00	0.16	0.32	0.65	0.75	-
	Feed	-0.03	-0.02	-0.01	0.00	0.01	0.84	100.00
	Feed * Treatment	-0.05	-0.03	-0.02	0.00	0.02	0.83	100.00
	Feed * Edge	0.00	0.00	0.00	0.00	0.00	0.88	100.00
	Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.63	100.00

Table 2.9. Logistic regression results and credible intervals for Timber rattlesnake (*Crotalus horridus*) random walk and 2<sup>nd</sup> order resource selection functions for study 2 in year 2019. Intercept denotes the effect of the broadcast-fed treatment on females.

Method	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
Random Walk	Intercept	-1.63	-1.48	-1.41	-1.34	-1.18	1.00	-
	Edge	0.07	0.11	0.13	0.15	0.19	1.00	0.00
	Treatment	-0.87	-0.62	-0.49	-0.36	-0.10	0.99	-
	Feed	-0.04	-0.03	-0.03	-0.02	-0.01	1.00	100.00
	Feed * Treatment	0.04	0.05	0.06	0.07	0.09	1.00	12.25
	Feed * Edge	-0.02	-0.02	-0.01	-0.01	-0.01	1.00	100.00
	Feed * Edge * Treatment	-0.01	-0.01	-0.01	0.00	0.00	0.96	100.00
Traditional 2nd Order	Intercept	-1.53	-1.30	-1.19	-1.08	-0.83	1.00	-
	Edge	-0.06	-0.02	0.00	0.02	0.07	0.54	98.60
	Treatment	-0.83	-0.42	-0.23	-0.05	0.34	0.80	-
	Feed	-0.06	-0.05	-0.04	-0.03	-0.02	1.00	82.62
	Feed * Treatment	0.01	0.03	0.04	0.05	0.07	0.99	80.44
	Feed * Edge	-0.02	-0.01	-0.01	0.00	0.00	0.99	100.00
	Feed * Edge * Treatment	-0.01	-0.01	0.00	0.00	0.01	0.78	100.00

Table 2.10. Logistic regression results and credible intervals for Timber rattlesnake (*Crotalus horridus*) 3<sup>rd</sup> order resource selection in relation to feeder-fed and broadcast-fed treatments in study 2 in year 2019. Intercept denotes the effect of the broadcast-fed treatment on females.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value	ROPE %
90%	Intercept	-1.94	-1.69	-1.57	-1.46	-1.22	1.00	-
	Edge	-0.08	-0.02	0.00	0.03	0.08	0.53	87.82
	Treatment	-0.34	0.07	0.29	0.49	0.94	0.82	-
	Feed	-0.03	-0.01	0.00	0.01	0.02	0.62	100.00
	Feed * Treatment	-0.04	-0.02	-0.01	0.01	0.03	0.62	100.00
	Feed * Edge	-0.01	0.00	0.00	0.00	0.01	0.62	100.00
	Feed * Edge * Treatment	-0.02	-0.01	-0.01	-0.01	0.00	0.98	100.00
50%	Intercept	-2.16	-1.87	-1.73	-1.59	-1.32	1.00	-
	Edge	-0.12	-0.05	-0.01	0.03	0.09	0.57	71.20
	Treatment	-0.48	0.05	0.30	0.54	1.05	0.79	-
	Feed	-0.02	0.00	0.02	0.03	0.05	0.79	100.00
	Feed * Treatment	-0.08	-0.04	-0.02	0.00	0.03	0.80	86.40
	Feed * Edge	-0.01	0.00	0.00	0.01	0.02	0.57	100.00
	Feed * Edge * Treatment	-0.02	-0.01	-0.01	0.00	0.01	0.88	100.00

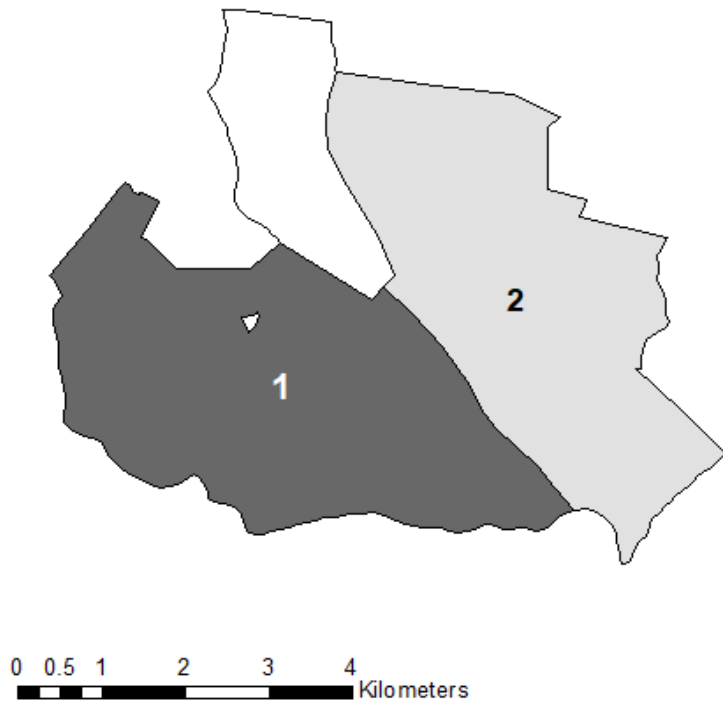


Figure 2.1. Feeding treatments on Di-Lane Wildlife Management Area, located in Waynesboro, GA. Treatment 1 indicates the unfed treatment in 2018 and the broadcast-fed treatment in 2019. Treatment 2 indicates the feeder fed treatment in both years.

## Black Rat Snake Resource Selection - Study 1

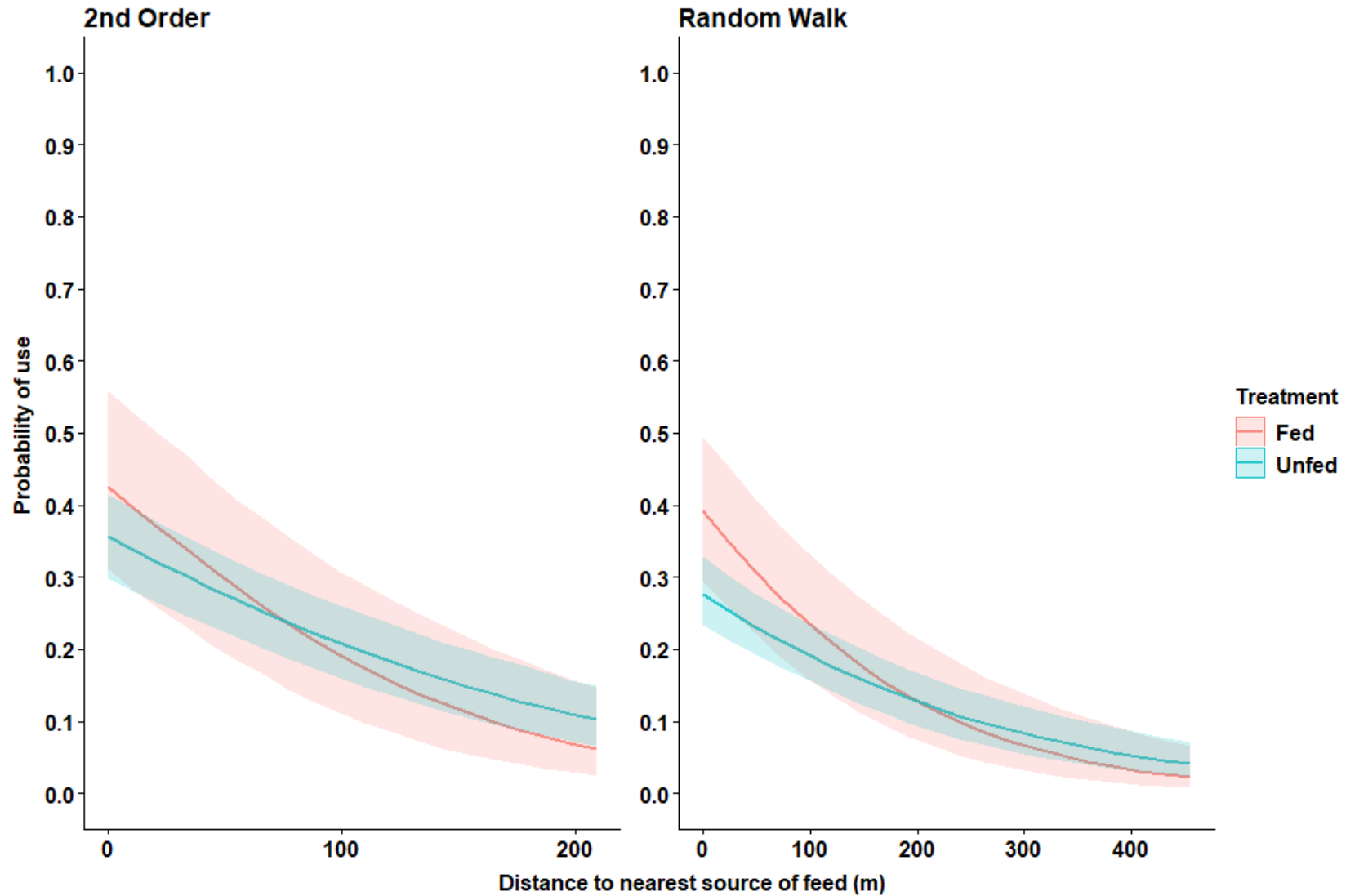


Figure 2.2. Random walk and 2<sup>nd</sup> order resource selection model predicted Black rat snake (*Pantherophis obsoletus*) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.



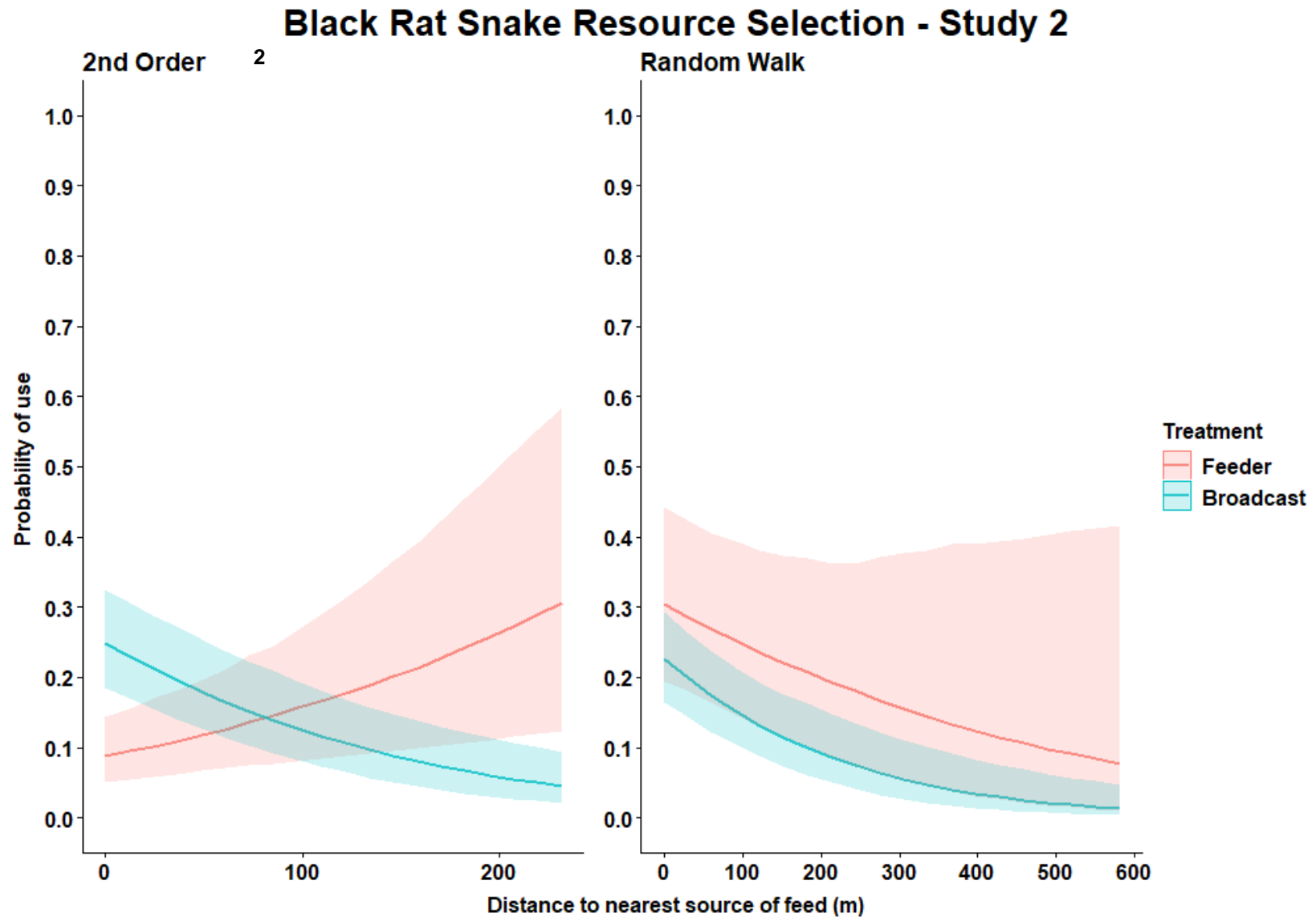


Figure 2.3. Random walk and 2<sup>nd</sup> order resource selection model predicted Black rat snake (*Pantherophis obsoletus*) mean probability of use as a function of distance to feeder in fed and broadcast treatments during study 2 in 2019.

## Timber Rattlesnake Resource Selection - Study 1

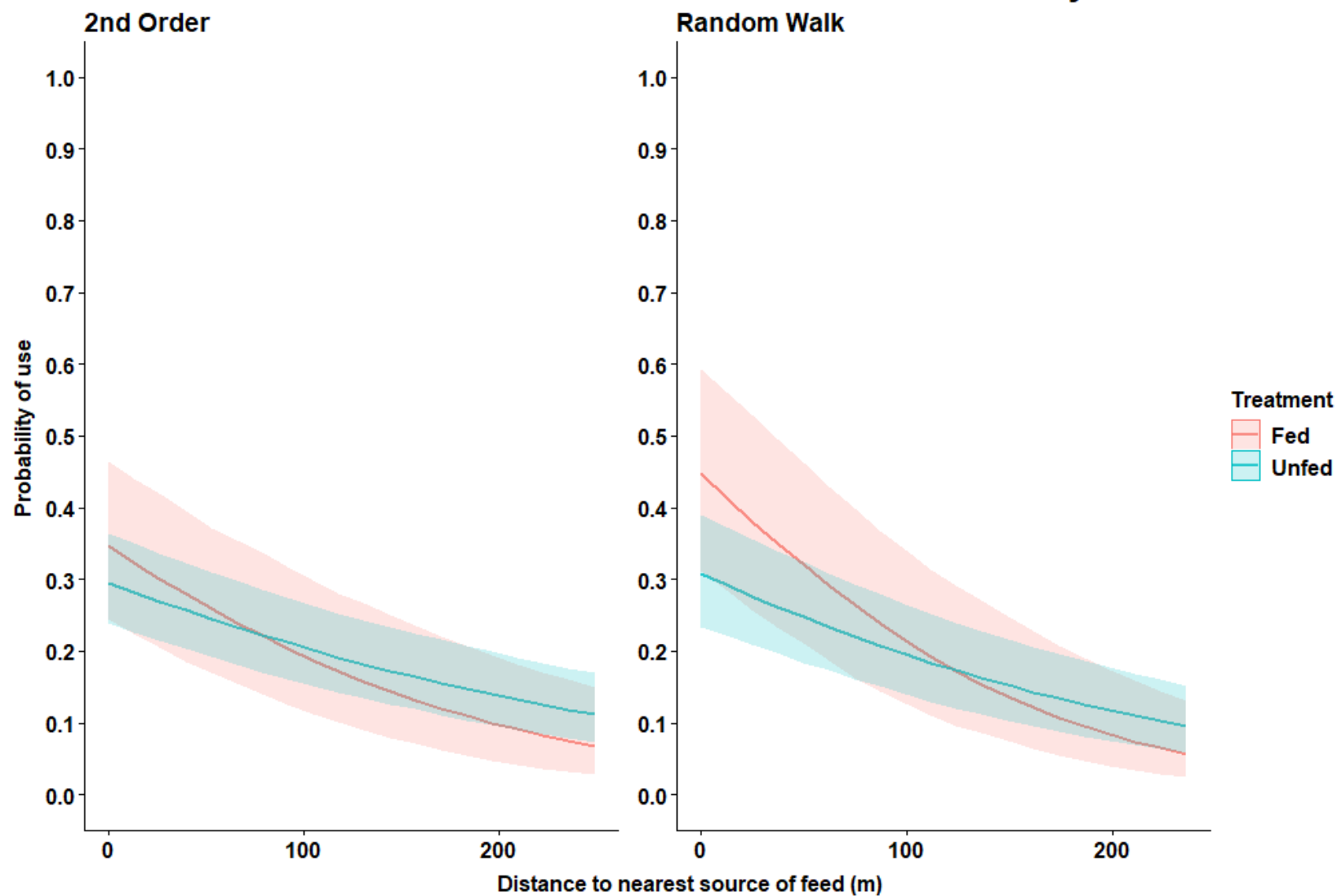


Figure 2.4. Random walk and 2<sup>nd</sup> order resource selection model predicted Timber rattlesnake (*Crotalus horridus*) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.

## Timber Rattlesnake Resource Selection - Study 2

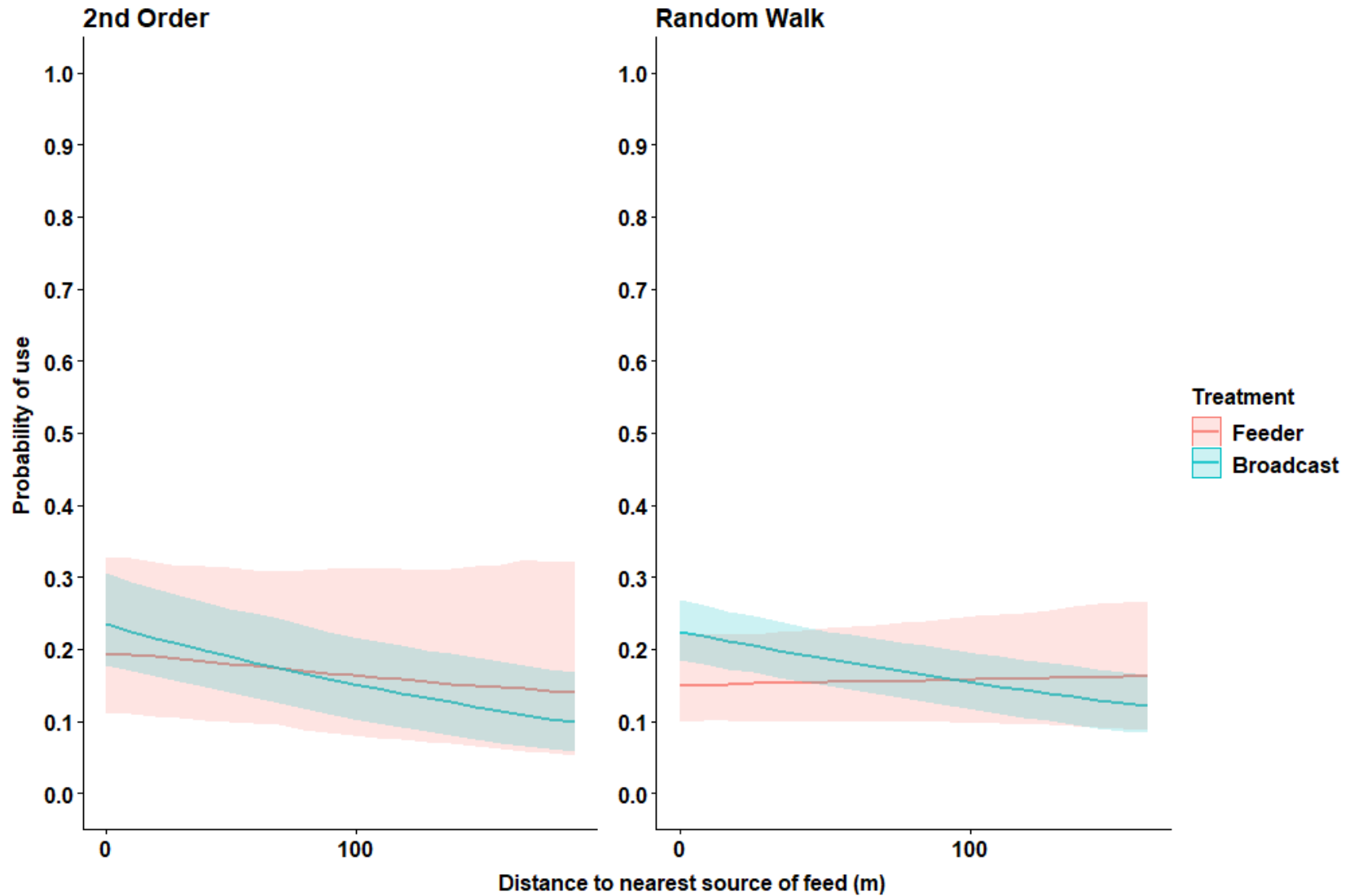


Figure 2.5. Random walk and 2<sup>nd</sup> order resource selection model predicted Timber rattlesnake (*Crotalus horridus*) mean probability of use as a function of distance to feeder in fed and broadcast treatments during study 2 in 2019.

CHAPTER 3

EFFECT OF FOOD DISTRIBUTION ON RESOURCE SELECTION OF NORTHERN  
BOBWHITE (*COLINUS VIRGINIANUS*)<sup>2</sup>

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<sup>2</sup> Gardner, R.R., Terhune II, T.M., Maerz, J.C., Martin, J.A. To be submitted to *The Journal of Applied Ecology*

## 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 bobwhites to concentrate their movements closer to feed than others, thereby altering the potential for predator-prey interactions near feed. We used radio-tracked locations and movements within areas with stationary feeders (“feeder fed”) and non-supplementally fed (“unfed”; study 1, year 1) or non-stationary “broadcast-fed” (study 2, year 2) areas to compare resource selection within a Bayesian framework. Second and 3<sup>rd</sup> order resource selection functions indicated bobwhite were more likely to occur in proximity to feeders and feedlines when available, but Northern 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 non-target predator and target prey species.

## INTRODUCTION

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 (Olton et al., 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.

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 many are concerned increased predator presence may have 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. Alternatively, while 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. As a result, different feeding techniques may uniquely alter the distributions of risk, resulting in differences in resource selection patterns that could influence the potential for predator-prey interactions.

Northern Bobwhite (*Colinus virginianus*; hereafter referred to as bobwhite) are fast pace of life, ground-dwelling birds endemic to the United States and a widely popular game species (Guthery, 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. Supplemental feeding is used by land managers 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 not directly negatively affect bobwhite survival (Townsend et al., 1999; Sisson et al., 2000), increased perceived risk may impact 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 (Miller et al., 2017; Wellendorf et al., 2017), and the distribution of supplemental feed and the subsequent distribution of risk likely impacts breeding individuals.

The objective of this study was to determine how two different methods of distributing supplemental feed affected the resource selection of bobwhites. We compared bobwhite resource selection within two 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 (Study 2).

### *Hypotheses and Predictions*

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 bobwhites in the feeder-fed treatment bobwhites would select for 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 bobwhites. Although 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), 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 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.

## **METHODS**

### *Study Area*

Di-Lane Wildlife Management Area, hereafter referred to as Di-Lane, is managed for the growth of early successional habitat with a management emphasis on Northern Bobwhite. Di-Lane is located in the Upper Coastal Plains of Burke County, Georgia and is made up of roughly



3,300 ha of federally owned land. Prominent species of vegetation and land cover types include a mixture of fallow fields [mostly camphorweed (*Heterotheca subaxillaris*), common ragweed (*Ambrosia artemisiifolia*), partridge pea (*Chamaecrista fasciculata*), annual low panic grasses (*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 2-3 years and implemented biannual meso-mammal predator control and year-round supplemental feeding of sorghum (*Sorghum bicolor*). Average temperatures for Burke County, Georgia range from 31.6 to 15 °C in May and 33.3 to 19.4 °C in June through August. Average rainfall is approximately 6.4 cm in the month of May and ranges from 12.6 to 13.4 cm in months June through August (National Climate Data Center, National Oceanic and Atmospheric Administration).

### *Experimental Design*

A total of 223 feeders, where an average of 7 feeders were located an average of 175 m apart per every 100 h<sup>2</sup> of non-forested land, were within our treatments throughout both study years and were initially installed in 2008. Most feeders were within patches of scrub shrub and covered with medium to high density vegetation on all sides. All distribution of supplemental feed within feeders and along feedlines was carried out by the Georgia DNR.

### *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 (1501 ha) and filled all feeders within the treatment ( $n = 131$ ) with sorghum on June 12th, 2018. The unfed treatment was assigned to a treatment area on the western half (1501 ha) and all feeders within the treatment ( $n = 92$ ) were emptied of any remaining feed and left in place on the same day (Figure 3.1). The fill level of ten random feeders within the fed treatment were 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 3.1). We checked the fill level of ten random feeders within the feeder-fed treatment every week, and feeders were refilled when necessary. Beginning May 20<sup>th</sup>, 2019, sorghum was broadcast along predetermined routes (100 – 300 m apart) along pre-existing roads and firebreaks and averaged roughly 3.25 km of feedline per 100 h<sup>2</sup>. Feed was spread once every two weeks as described by Buckley et al. (2015) along approximately 63 km of feed lines at a rate of 5.38 bushels/ha/yr and at an average width of 13 m. Before our field season began, feeders were full within the broadcast-fed treatment during turkey hunting season, between March 21<sup>st</sup> and May 15<sup>th</sup> of 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 emptied following turkey season, but we found 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 between 250-300 m apart throughout feeding treatments (Stoddard, 1931). Trapping occurred over the course of two weeks in late February to early March in years 2018 and 2019. All unique individuals were weighed, sexed, aged, and given unique number leg bands (National Band & Tag Company) upon capture. Individuals with a body mass  $\geq 130$  g were fitted with Very High Frequency (VHF) radio transmitters (Holohil Systems Corp, Ontario, Canada and American Wildlife Enterprises, Monticello, FL, USA). Caution was taken to deploy transmitters equally across the study site and within feeding treatments, and between 60 to 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).

### *Radio Telemetry*

Bobwhite were relocated 5 to 7 days a week using Biotracker receivers and 3-element directional antennae from Lotek Wireless Inc. (Newmarket, ON, 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 three days in a row were relocated from within 3 – 5 m of the bird to visually confirm if 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 analyses only included data collected when supplemental feed was being reliably distributed within each designated treatment, only data gathered between dates June 12<sup>th</sup>, 2018 – Sept 1<sup>st</sup>, 2018 and May 20<sup>th</sup>, 2019 – Sept 7<sup>th</sup>, 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 (Kellner, 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 in order to obtain successful chain convergence as well as 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 below 1.1 (Gelman et al., 2004). Values of all estimated parameters had an R-hat value of 1.1 or below, and further visual inspection of trace plots confirmed chain convergence. We reported posterior means, 95% and 50% credible intervals, 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 ranging from -.025 to .025 (Kruschke, 2014). Partial overlap between the ROPE and posterior distribution indicated 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 study species' selection of supplementally fed areas as well as 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 chapter two. We modeled RSFs at 2<sup>nd</sup> (i.e., selection of home ranges) and 3<sup>rd</sup> order (i.e., selection of resources within each home range) scales as described by Johnson (1980). Adequate area coverage is important when generating available locations (Buskirk and Millspaugh, 2006). Since 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 3<sup>rd</sup> order selection scale (Appendix B). We generated random points within each individual's home range equal to five times the number of telemetry relocations recorded for each individual. For 2<sup>nd</sup> 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 (ESRI 2019) and buffered them by their average daily movement distance. Euclidean distance to each land cover types of interest (forest edge, scrub shrub, and feeder or feedline depending on treatment) of all used and available locations was then calculated using the Generate Near Table tool in ArcGIS (ESRI 2019).

We analyzed resource selection trends 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/variance). We used vague normal priors for fixed effects (mean = 0, sd = 0.001). Distance related numerical predictors were divided by 10 to make a more meaningful output. Non-distance 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:

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

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

$$\beta_{0,j} \sim \text{Norm}(\mu, \tau);$$

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

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

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,  $k = 1, 2, \dots$  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 3.1.

## RESULTS

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

A total of 26 individuals were used in our analyses of year 2018 data, 14 (8 F, 6 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 3.2, Figure 3.2); however, for every 10 m increase in distance to feeder, probability of use decreased by 7% (Bayesian  $P$ -value = 1.00, Table 3.2). In addition, for every 10 m increase in distance to scrub shrub, probability of use decreased by 33% (Bayesian  $P$ -value = 1.00, Table 3.2). 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 3.3, Figure 3.3). Additionally, for every 10 m increase in distance to scrub shrub, probability of use decreased by 31% (Bayesian  $P$ -value = 1.00, Table 3.3). Within their 50% KUD core use areas, bobwhites selected for areas closer to feeders within the feeder-fed treatment (Bayesian  $P$ -value = 1.00, Table 3.3), where bobwhites within the unfed

treatment were much more likely to select for areas farther from feeders than feeder-fed bobwhite (Figure 3.4).

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

A total of 35 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, Table 3.4 & Table 3.5), though the effect size of the interaction between distance to feeder and treatment was somewhat small within their 50% core use areas (Figure 3.5, Figure 3.6, Figure 3.7). In addition, bobwhite 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 3.4), by 21% within their 90% home ranges (Bayesian  $P$ -value = 1.00, Table 3.5), and by 23% within their core use areas (Bayesian  $P$ -value = 1.00, Table 3.5).

## **DISCUSSION**

We found support for our hypothesis that resource selection of feeder-fed and broadcast-fed bobwhites differed. Bobwhites on all scales selected for areas closer to feed sites; however, bobwhites were more likely to select for areas closer to feeders than feedlines. In agreement with previous studies, this suggests bobwhite viewed areas near supplemental feed as higher quality foraging patches regardless of both the presence of natural food resources and distribution method (Landers and Mueller, 1986; Sisson et al., 2000; Doerr and Silvy, 2002; Guthery et al., 2004; 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 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 resource patches than feedlines. It is also possible bobwhite selected for areas closer to feeders simply due to the spatial distribution of feeding sites, where feeders are single points versus feedlines which are continuous bands of feed. Nevertheless, 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 in comparison. Regardless of feed distribution, fed sites may then act as ecological traps (Gates and Gysel, 1978). 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 suggests bobwhites likely forage near feeders and may view fed sites as higher quality foraging patches (Johnson, 1980). 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. Regardless, an increase in overall bobwhite density and concentration near feeders may increase the overall probability of predators focusing their foraging efforts near feed interacting with bobwhite.

The spatial context of the feed source location in respect to shrub cover and forest edge did not play a role in selection of fed areas. However, distance to shrub cover had a relatively strong impact on bobwhite resource selection in both study years at most selection scales. Bobwhites likely incorporate shrub cover 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 shrub cover between treatments, it is possible 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 bobwhite use of shrub cover when exposed to different feeding treatments.

Due to the un-replicated 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 as a result. Our research also implies that bobwhite may select for areas near feeders months after feeding was discontinued, suggesting managers may benefit from periodically altering the location of feeders and feedlines to keep target species from getting habituated to foraging in specific locations. 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 alternative 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 predation. Finally, the distribution of supplemental feed may impact 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 and brood-rearing individuals as well as winter coveys.

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## TABLES AND FIGURES

Table 3.1. Description of covariates used in RSF analyses in years 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
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,
Feed * SS * Treatment	Interaction between distance to nearest fed area, distance to scrub shrub,

Table 3.2. Logistic regression results and credible intervals for Northern Bobwhite (*Colinus virginianus*) 2<sup>nd</sup> order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females.

Parameters	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

Table 3.3. Logistic regression results and credible intervals for Northern Bobwhite (*Colinus virginianus*) 3<sup>rd</sup> order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian P-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

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Table 3.4. Logistic regression results and credible intervals for Northern Bobwhite (*Colinus virginianus*) 2<sup>nd</sup> 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.

Parameters	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

Table 3.5. Logistic regression results and credible intervals for Northern Bobwhite (*Colinus virginianus*) 3<sup>rd</sup> 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.

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

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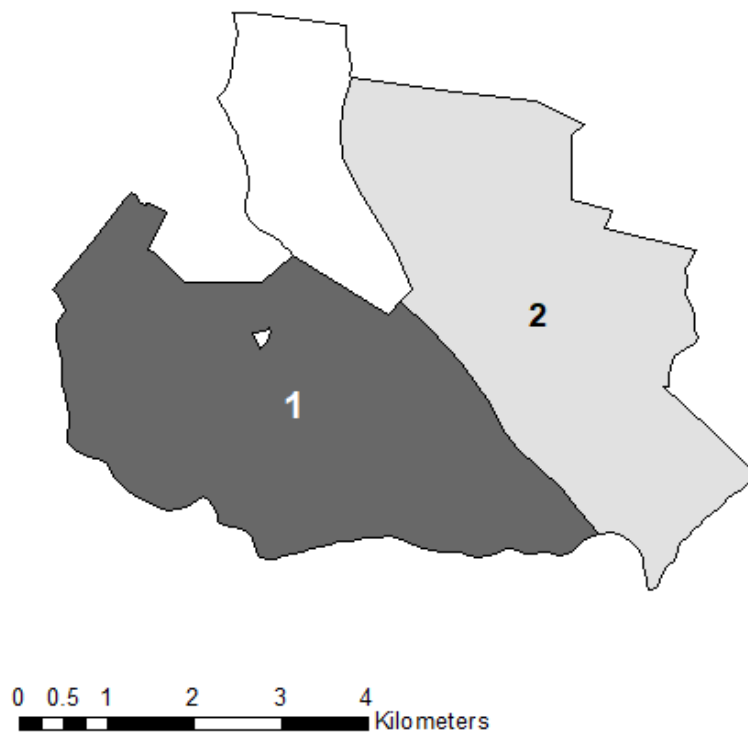


Figure 3.1. Feeding treatments on Di-Lane Wildlife Management Area, located in Waynesboro, GA. Treatment 1 indicates the unfed treatment in 2018 and the broadcast-fed treatment in 2019. Treatment 2 indicates the feeder fed treatment in both years.



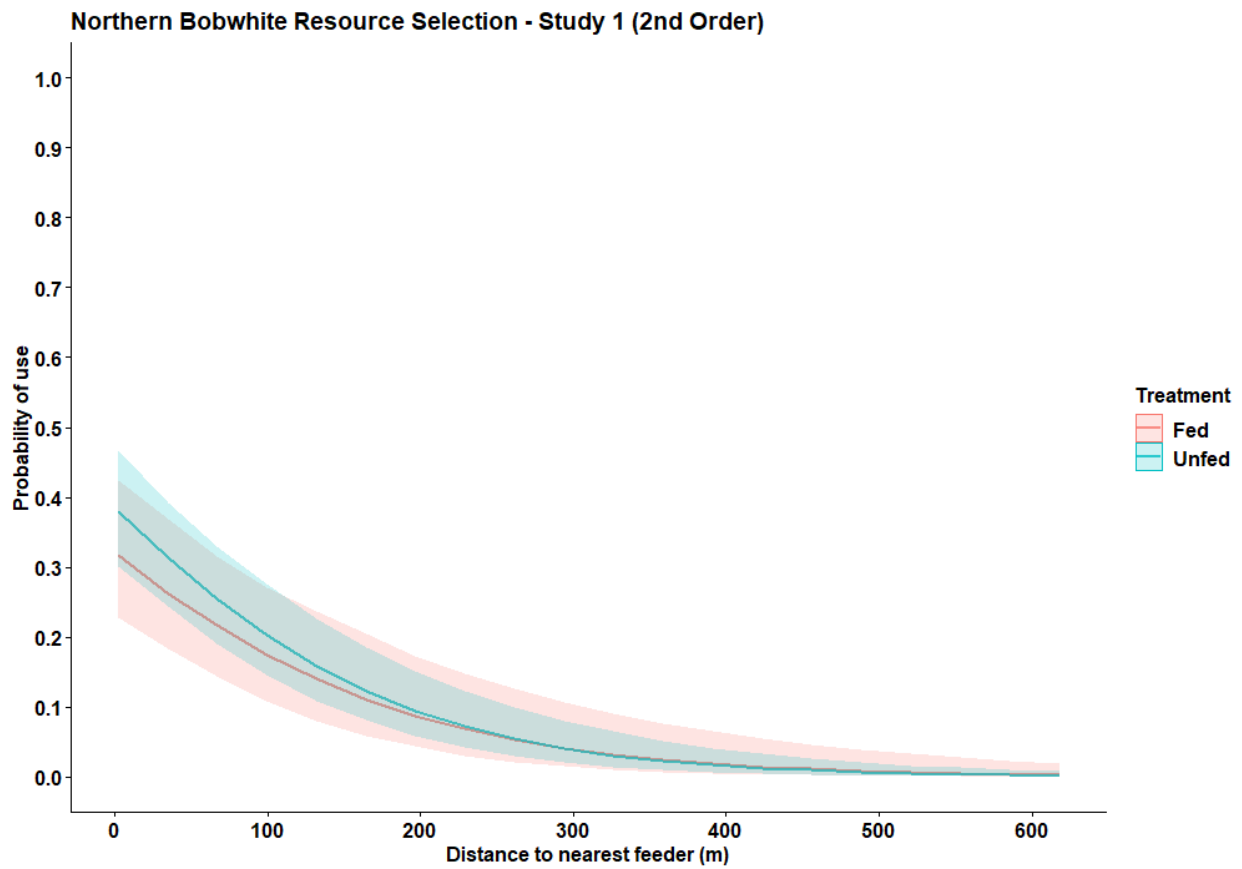


Figure 3.2. 2<sup>nd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.

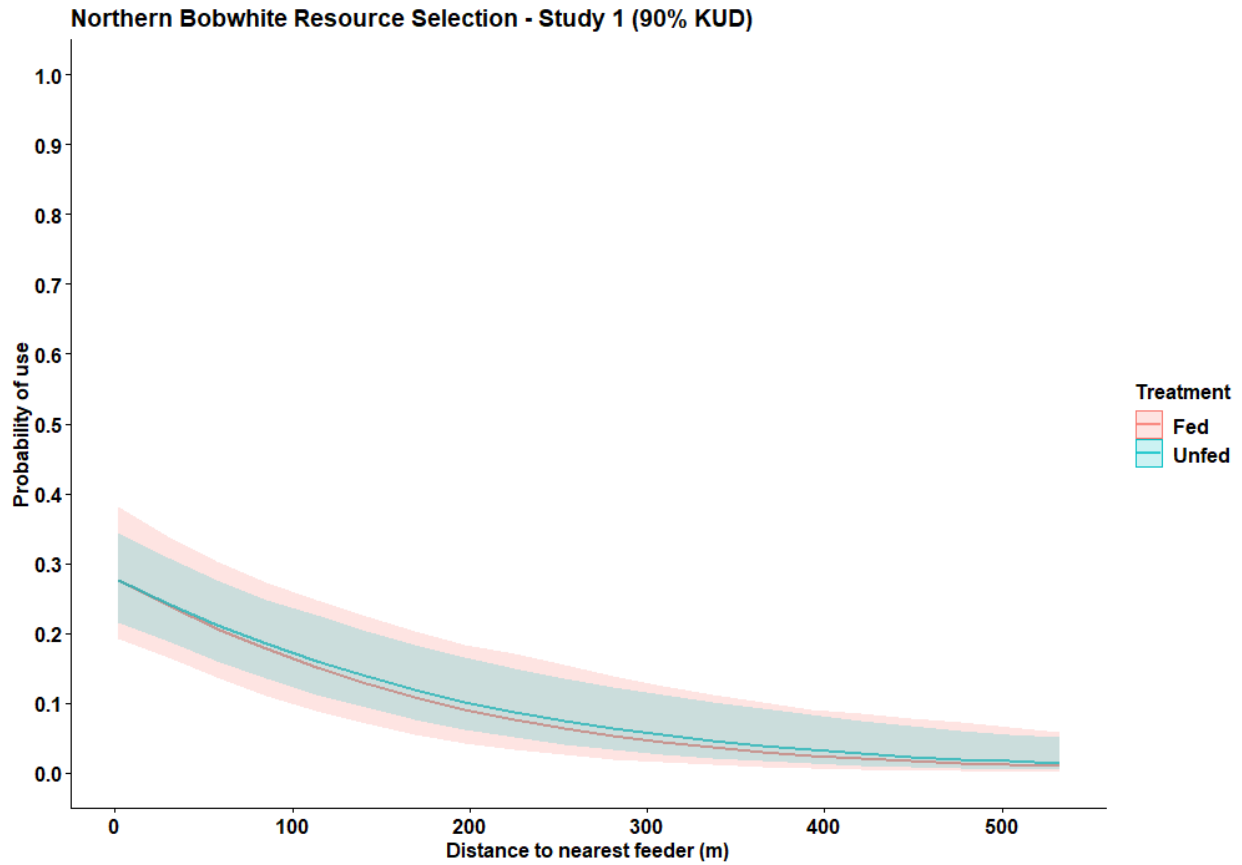


Figure 3.3. 3<sup>rd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 90% home ranges.

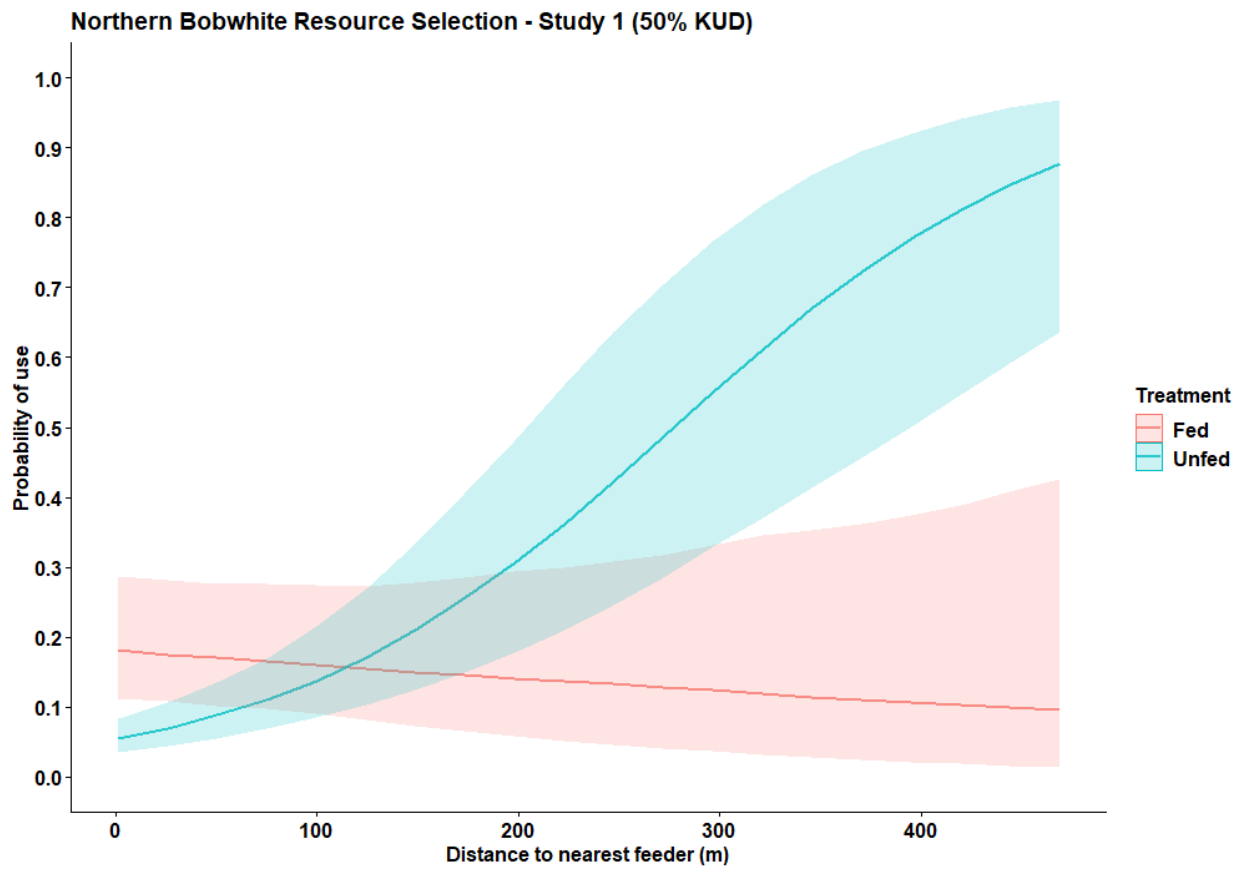


Figure 3.4. 3<sup>rd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 50% core use areas.

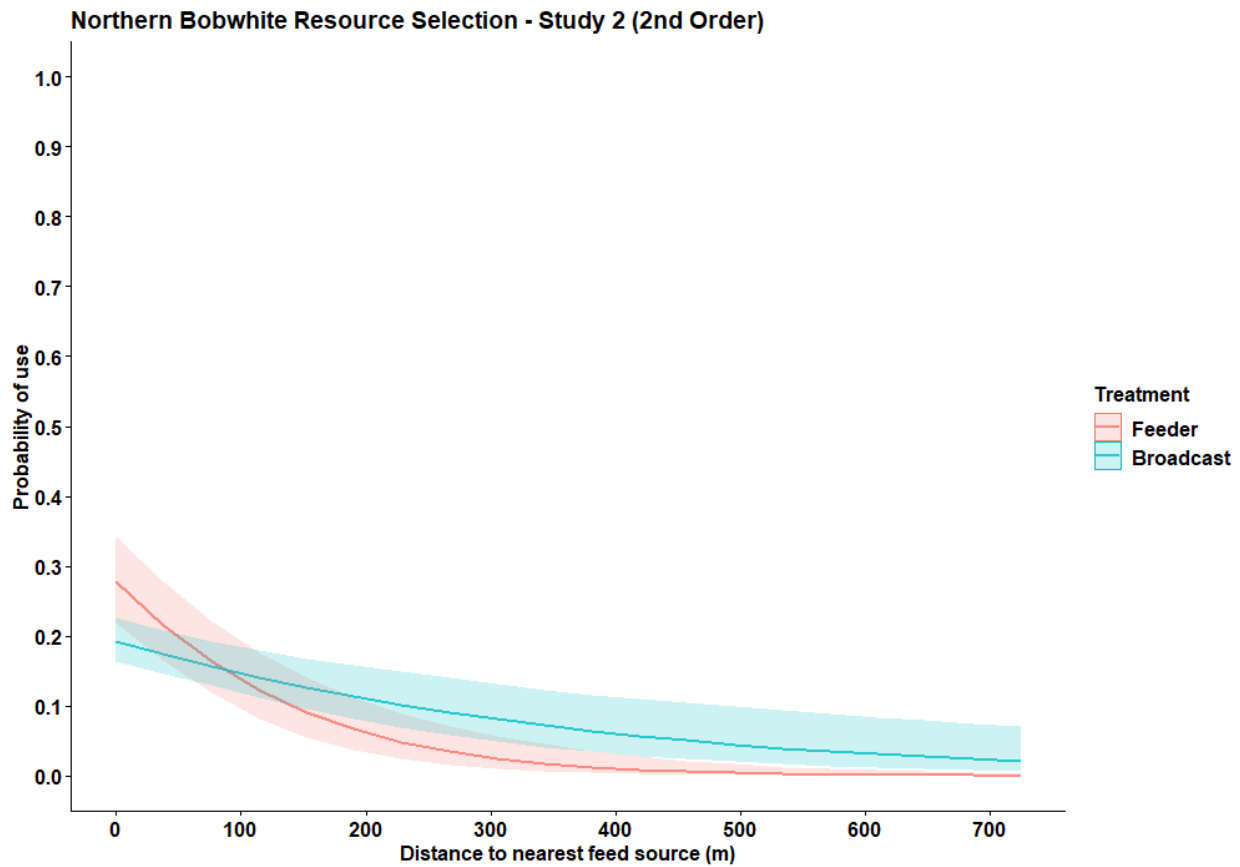


Figure 3.5. 2<sup>nd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019.

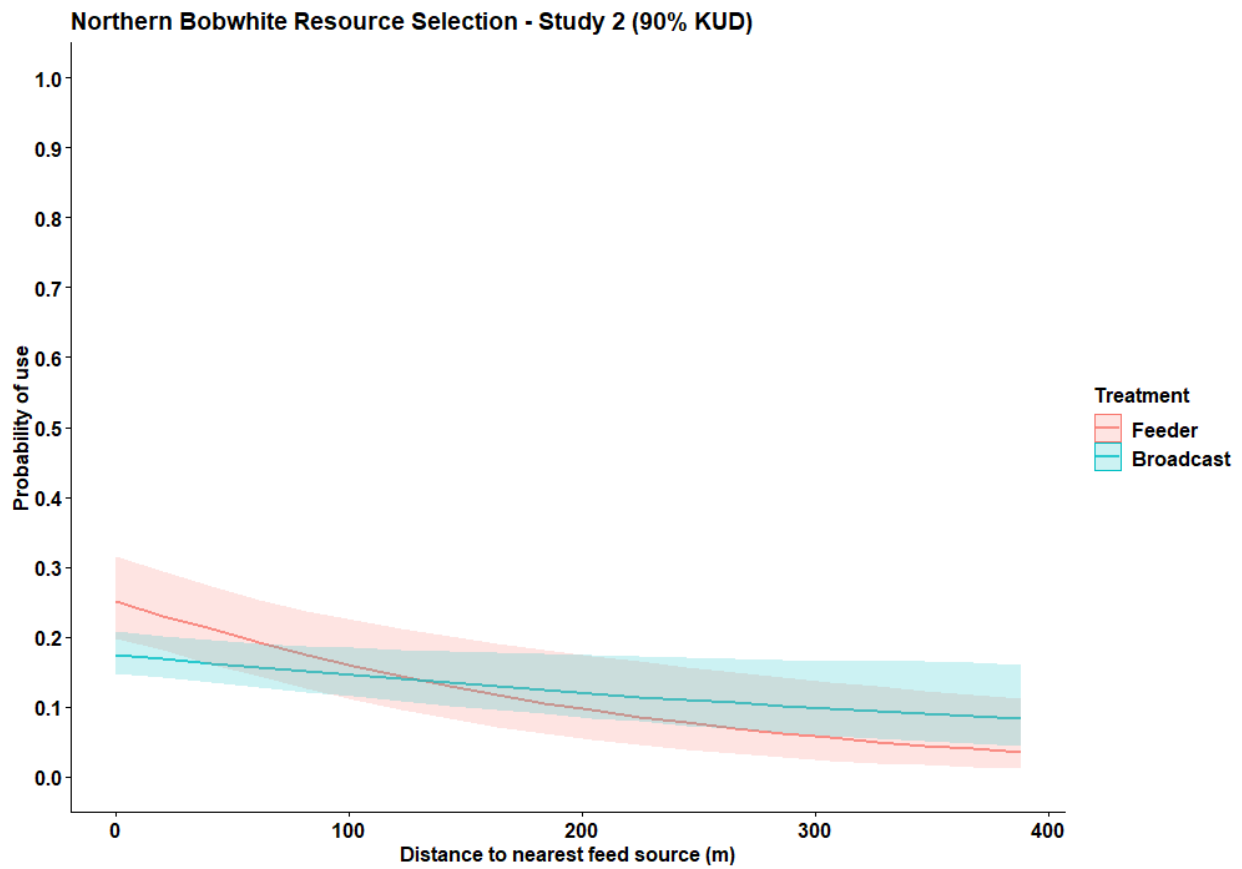


Figure 3.6. 3<sup>rd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 90% home ranges.

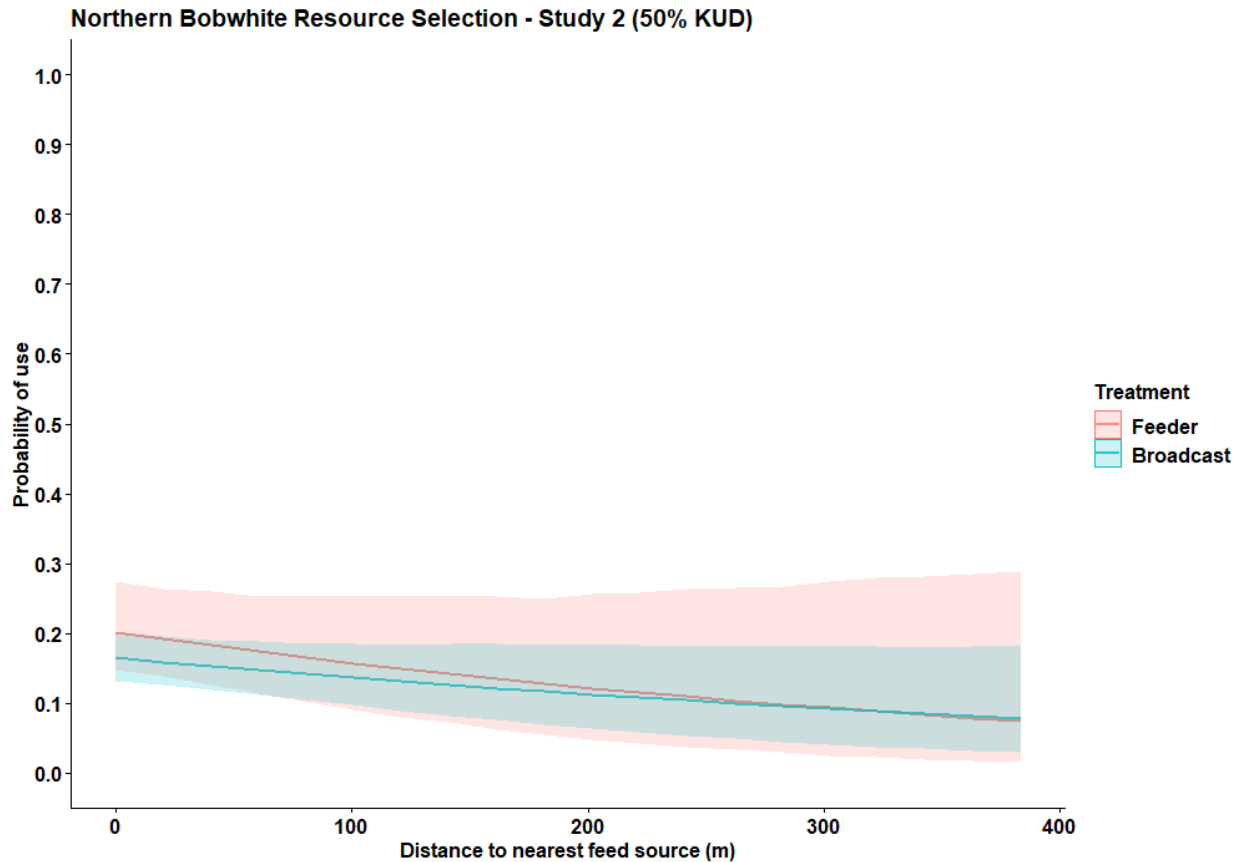


Figure 3.7. 3<sup>rd</sup> order resource selection model predicted Northern Bobwhite (*Colinus virginianus*) mean probability of use as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 50% core use areas.

## CHAPTER 4

### SYNTHESIS AND MANAGEMENT IMPLICATIONS

Through this research, I determined that Timber rattlesnakes and Northern Bobwhites select for areas near supplemental feed regardless of distribution method, though bobwhites were more likely to be closest to filled feeders in comparison to feedlines while Timber rattlesnakes were closest to feedlines on the landscape scale. However, Black rat snakes may not necessarily forage closer to fed sites. This generally suggests bobwhites and Timber rattlesnakes likely viewed areas around supplemental feed as higher quality foraging areas. This also implies different distributions of food resources can alter the potential for predator-prey interactions. Bobwhite foraging in fed areas may be more likely to interact with a Timber rattlesnake than in unfed areas, and Timber rattlesnake density may increase more with the use of feedlines, creating a greater overall chance of interaction than in a feeder-fed area. While broadcast-fed bobwhites may spend less time near feedlines and have a lesser overall chance of interacting with predators focusing their foraging efforts near them compared to feeders, a higher density of predators may be able to be supported within a broadcast-fed area than a feeder-fed area due to a larger amount of feed being distributed across the landscape. As a result, the distribution of risk across a landscape may be uniquely affected depending on distribution methods used, and there may be a trade-off involved for managers utilizing supplemental feed. In addition, our research also implies that both predator and prey may select for areas near feeders months after feed was no longer being distributed, suggesting managers may benefit from periodically altering the location of feeders and feedlines to keep predator and prey from getting habituated to hunting in specific locations.

Additionally, although managed species may be more likely to encounter predators near feed, they may also be ignored for other, more preferred prey, or only act as alternative prey when preferred prey is not present. It is also possible overall bobwhite survival would not be greatly affected by greater Timber rattlesnake densities considering snakes are not their primary predators. However, the presence of snakes near feed would likely increase their chances of encountering humans, and technicians charged with distributing supplemental feed may have a higher chance of interacting with a Timber rattlesnake near feeders than near feedlines. It is unclear whether our study species were more likely to encounter certain predators near supplemental feed, and future research should attempt to quantify the effect of food distribution on the frequency of predator-prey interactions and subsequent survival of species of interest.

In conclusion, implementing broadcast feeding may diminish the concentration of foraging efforts of bobwhites near feed but may increase the density of Timber rattlesnakes. However, implementing feedlines instead of feeders may also decrease possible interactions between humans and Timber rattlesnakes. The comparative impact of different distribution methods of supplemental feed on bobwhite and snake survival is unknown, and further research is necessary to understand the full impact food distribution may have. This study is the first to examine how different distributions of supplemental food resources affects the resource selection of snakes and their prey simultaneously. Further investigation of the impacts different distributions of supplemental feed have on managed species and their predators will provide greater understanding of predator-prey relationships driven by food resources and the wide ranging impacts of food resource distribution on each trophic level, informing and improving management efforts in the process.



## APPENDECES

## A

### *Snake Home Range Analyses*

We estimated fixed kernel density home ranges (50% and 90% isopleths) for individual snakes using r package “adehabitatHR” (Worton, 1989; Börger et al., 2002; Calenge, 2019). Although the least-squares cross-validation method is recommended for bandwidth selection in ecological studies (Worton, 1995; Seaman and Powell, 1996; Seaman et al., 1999), our snakes often spent several consecutive days in the same location, and our home range estimates did not converge using this method. The default bandwidth ( $h_{ref}$ ) resulted in large, oversmoothed kernels. We instead used a single smoothing parameter ( $h$ ) for each species, subjectively chosen based on successive trials to produce what visually appeared to be the most representative home ranges.

In an attempt to identify the minimum number of locations necessary to obtain an accurate home range estimate, we graphed home range area curves for each individual to visually determine when each curve reached an asymptote (Bond et al. 2001). However, most snakes either never reached an asymptote or, after initially leveling off, their home range size would increase near the end of the study period. As a result, we incorporated the number of locations used to estimate home range as an additional parameter in the model. To ensure the number of locations used in home range estimation did not affect home range size, we incrementally increased the number of locations required for individuals to be included in the analysis until the average effect size was  $<0.2$  with resulting 50% credible intervals overlapping zero. We recognize that these may not be considered unbiased home range estimates as defined by other studies in which individuals reach a stable home range within the study period (Odum and Kuenzler 1955; Bond et al., 2001; Haines et al. 2006; Laver and Kelly, 2008); however, we believe these estimates represent the area traveled by an individual during its normal activities

such as resting, foraging, and mating within the span of the study period, and is therefore still an appropriate metric to use to measure the effect of supplemental feed on space use.

We used a single global model for each snake species to estimate the effects of feeding treatment on Timber rattlesnake and Black rat snake home range size. Sex, SVL, and the number of independent fixes were included as parameters in all home range models (Weatherhead and Hoysak, 1989; Carfagno, 2008; Fitch, 1963; Durner and Gates, 1993; Macdonald et al. 1980,). The 90% home range polygons of two Black rat snakes in the broadcast feeding treatment overlapped with at least one of the eleven stationary feeders discovered to have feed after turkey hunting season; therefore, we included an additional variable indicating whether a snake had been exposed to multiple feeding approaches during the 2019 field season.

We performed a separate linear regression using a log-normal distribution for each species in 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:

$$\mu_j = \beta_0 + \beta_{j,treatment} + \beta_{j,sex} * X_{sex} + \beta_{j,svl} * X_{svl} + \beta_{j,loc\_freq} * X_{loc\_freq} + \beta_{j,fill} * X_{fill}$$

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

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

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

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

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

are model priors. The model was fitted for  $i = 1, 2, \dots, N$  where  $N$  represents the total number of observations, while  $j = 1, 2, \dots, n$  denotes the number of individuals, and  $k = 1, 2, \dots$  number of fixed effects. Here *HRsize* represents the home range size for individual  $j$ .  $\beta_0$  represents the overall mean home range size.  $B_{\text{treatment}}$  represents the effect of feeding treatment.  $B_{\text{sex}}$  characterizes the effect of sex.  $B_{\text{svl}}$  symbolizes the effect of SVL.  $B_{\text{sex*svl}}$  denotes the interaction of sex and SVL.  $\beta_{\text{loc\_num}}$  characterizes the effect of the number of locations used to estimate home range.  $B_{\text{fill}}$  represents the effect of having been exposed to more than one feeding treatment.  $X$  represents the response variable for each respective fixed effect noted.

### *Black Rat Snake Results*

#### *Study 1: Feeder-fed Treatment vs Unfed Control Treatment*

It was unlikely there was any difference between feeding treatments in home range area estimates of 50% or 90% isopleths (Bayesian  $P$ -value = 0.63 and 0.56 respectively, Table 3.6, Table 3.8). Similarly, SVL was unlikely to have affected the size of either home ranges (90% KUDs) or core use areas (50% KUDs) (Bayesian  $P$ -value = 0.61 and 0.67 respectively, Table 3.6); however, males had 77% larger home ranges and 55% larger core use areas than females (Bayesian  $P$ -value = 0.97 and 0.93 respectively, Table 3.6, Table 3.9).

#### *Study 2: Feeder-fed Treatment vs Broadcast-fed Treatment*

It was unlikely that there was any difference in home range estimates of either the 50% or 90% KUDs between the feeder-fed treatment and the broadcast-fed treatments (Bayesian  $P$ -value = 0.57 and 0.70 respectively, Table 3.7, Table 3.7). It was also unlikely there was any difference between male and female home range estimates (Bayesian  $P$ -value = 0.54 and 0.76 respectively, Table 3.7, Table 3.8) or the number of feeding treatments snakes were exposed to in either the

50% or 90% isopleths (Bayesian  $P$ -value = 0.61 and 0.63 respectively, Table 3.6). Larger snakes tended to have larger 90% home ranges where, for every 15 cm increase in SVL, home range size increased by 16% (Bayesian  $P$ -value = 0.70, Table 3.6). SVL did not have an effect on 50% home range size (Bayesian  $P$ -value = 0.84, Table 3.6). The first-year home ranges of all three Black rat snakes tracked through both field seasons substantially overlapped (70% – 95%) with their second-year home ranges.

### *Timber Rattlesnakes Results*

#### *Study 1: Feeder-fed Treatment vs Unfed Control Treatment*

Timber rattlesnake home range estimates were 45% larger in the feeder-fed treatment than the unfed treatment (Bayesian  $P$ -value = 0.96, Table 3.9, Table 3.7). Similarly, estimates of core use areas were 48% larger in the feeder-fed treatment than in the unfed control (Bayesian  $P$ -value = 0.97, Table 3.9, Table 3.7). Larger snakes had larger home ranges and core use areas than smaller snakes. For every 19 cm increase in SVL, home range size increased by 60% (Bayesian  $P$ -value = 1.00, Table 3.9), and core use area increased by 28% (Bayesian  $P$ -value = 0.98, Table 3.10); however, sex was unlikely to have affected home range and core use area size (Bayesian  $P$ -value = 0.51 and 0.50 respectively, Table 3.9, Table 3.8).

#### *Study 2: Feeder-fed Treatment vs Broadcast-fed Treatment*

There was no clear effect of treatment on home range estimates of 50% or 90% isopleths (Bayesian  $P$ -value = 0.71 and 0.61 respectively, Table 3.9, Table 3.7). Larger snakes had larger 90% isopleths, where for every 9 cm increase in SVL, home range increased 25% (Bayesian  $P$ -value = 0.81, Table 3.9). Larger snakes also tended to have larger 50% core use areas, where core use area size increased by 34% for every 16 cm increase in SVL (Bayesian  $P$ -value = 0.89, Table 3.9).

Table 3.6. Linear regression results and credible intervals for Black rat snake (*Pantherophis obsoletus*) home ranges within feeding treatments each year. Intercept denotes the effect of the unfed treatment on females in 2018 and the effect of the broadcast-fed treatment on females in 2019.

Year	Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value
2018	50%	Intercept	0.21	0.60	0.76	0.92	1.32	0.99
		Treatment	-0.75	-0.13	0.13	0.38	0.99	0.63
		SVL	-0.35	-0.07	0.05	0.16	0.44	0.61
		Sex	-0.04	0.40	0.57	0.76	1.20	0.97
		Location Freq	-0.36	-0.12	-0.01	0.09	0.33	0.54
	90%	Intercept	1.64	2.05	2.21	2.38	2.77	1.00
		Treatment	-0.83	-0.19	0.06	0.33	0.97	0.56
		SVL	-0.32	-0.04	0.07	0.19	0.46	0.67
		Sex	-0.19	0.25	0.44	0.62	1.07	0.93
		Location Freq	-0.35	-0.09	0.01	0.11	0.36	0.51
2019	50%	Intercept	0.14	0.81	1.18	1.53	2.29	1.00
		Treatment	-0.45	-0.05	0.15	0.33	0.76	0.57
		SVL	-0.22	-0.02	0.07	0.16	0.33	0.84
		Sex	-0.44	0.01	0.21	0.42	0.86	0.54
		Location Freq	-0.20	0.00	0.10	0.20	0.40	0.70
	90%	Expose	-0.69	-0.13	0.13	0.40	0.95	0.61
		Intercept	1.47	2.21	2.56	2.93	3.76	0.98
		Treatment	-0.63	-0.15	0.05	0.26	0.69	0.70
		SVL	-0.17	0.05	0.15	0.25	0.46	0.70
		Sex	-0.71	-0.19	0.03	0.25	0.73	0.76
		Location Freq	-0.25	-0.02	0.08	0.18	0.41	0.76
		Expose	-0.79	-0.16	0.12	0.38	0.96	0.63

Table 3.7. Summary of Timber rattlesnake (*Crotalus horridus*) and Black rat snake (*Pantherophis obsoletus*) home ranges in each feeding treatment within both years of the study.

Year	Species	Kernel %	Treatment	n	Mean	SD	Lower Range	Upper Range
2018	Timber Rattlesnake	50	Unfed	6	3.16	1.16	1.58	4.46
			Feeder-fed	8	4.82	1.24	2.91	6.71
		90	Unfed	6	12.03	6.49	5.01	23.74
			Feeder-fed	8	17.16	7.31	4.93	26.38
	Black Rat Snake	50	Unfed	9	3.64	1.61	1.96	6.92
			Feeder-fed	3	2.98	1.09	1.91	4.08
		90	Unfed	9	13.85	1.61	8.73	24.35
			Feeder-fed	3	11.11	1.09	7.06	15.16
2019	Timber Rattlesnake	50	Broadcast-fed	4	4.66	1.33	3.65	8.85
			Feeder-fed	3	6.30	2.74	3.15	5.65
		90	Broadcast-fed	4	20.75	6.03	15.52	26.14
			Feeder-fed	3	17.17	7.31	11.25	25.29
	Black Rat Snake	50	Broadcast-fed	10	4.51	1.29	1.92	6.81
			Feeder-fed	7	5.43	2.69	3.08	10.30
		90	Broadcast-fed	10	15.82	5.47	6.24	25.13
			Feeder-fed	7	17.74	8.56	12.26	31.48

Table 3.8. Summary of male and female Timber rattlesnake (*Crotalus horridus*) and Black rat snake (*Pantherophis obsoletus*) home ranges within both years of the study.

Year	Species	Kernel %	Sex	n	Mean	SD	Lower Range	Upper Range
2018	Timber Rattlesnake	90	M	9	17.12	5.4	8.9	23.7
			F	5	11.09	9.01	4.9	26.3
		50	M	9	4.31	0.89	2.91	5.46
			F	5	3.48	2.36	1.58	6.71
	Black Rat Snake	90	M	8	15.17	5.25	10.14	24.35
			F	3	9.16	1.71	7.06	11.12
		50	M	8	4.09	1.44	2.66	6.92
			F	3	2.26	0.48	1.91	2.94
2019	Timber Rattlesnake	90	M	7	19.22	6.3	11.06	25.82
		50			5.6	2.26	3.15	8.84
	Black Rat Snake	90	M	11	17	6.57	11.31	31.48
			F	6	15.91	7.58	6.24	28.2
		50	M	11	5.08	1.99	3.52	10.31
			F	6	4.54	2.05	1.92	7.61



Table 3.9. Linear regression results and credible intervals for Timber rattlesnake (*Crotalus horridus*) home ranges within feeding treatments each year. Intercept denotes the effect of the unfed treatment on females in 2018 and the effect of the broadcast-fed treatment on females in 2019.

Year	Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian <i>P</i> -value
2018	50%	Intercept	0.71	1.00	1.12	1.24	1.53	1.00
		Treatment	-0.04	0.26	0.39	0.52	0.84	0.97
		SVL	0.02	0.18	0.25	0.32	0.47	0.98
		Sex	-0.55	-0.16	0.01	0.16	0.53	0.51
		Location Freq	-0.18	-0.03	0.04	0.10	0.25	0.66
	90%	Intercept	1.93	2.23	2.36	2.49	2.79	1.00
		Treatment	-0.07	0.24	0.37	0.51	0.82	0.96
		SVL	0.17	0.38	0.47	0.56	0.75	1.00
		Sex	-0.55	-0.17	0.00	0.17	0.54	0.50
		Location Freq	-0.26	-0.10	-0.02	0.05	0.23	0.58
2019	50%	Intercept	0.64	1.60	1.79	1.99	2.85	0.99
		Treatment	-2.55	-0.74	-0.32	0.08	2.04	0.71
		SVL	-0.37	0.16	0.29	0.44	1.09	0.89
		Location Freq	-1.43	-0.32	-0.09	0.14	1.17	0.61
	90%	Intercept	1.76	2.76	3.00	3.24	4.23	1.00
		Treatment	-2.73	-0.70	-0.20	0.30	2.44	0.61
		SVL	-0.66	0.06	0.23	0.40	1.10	0.81
		Location Freq	-1.48	-0.30	-0.02	0.26	1.45	0.52

## B

### *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., 2002; Calenge, 2019). 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 subjectively chosen based on successive trials to produce what visually appeared to be the most accurate home ranges. Bobwhite home ranges are commonly estimated for only those individuals with a minimum of 25 to 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, since 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 a minimum of 30 locations in both field seasons.

Along with treatment, we included covariates that would likely 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 (ESRI 2019). All home range polygons within fed treatments overlapped with supplemental feed; however, home ranges of two 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:

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

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

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

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

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

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

are model priors. The model was fitted for  $j = 1, 2, \dots, n$  denotes the number of individuals,  $k = 1, 2, \dots$  number of fixed effects. Here *HRsize* represents the home range size for individual  $j$ .  $\beta_0$  represents the intercept.  $B_{\text{treatment}}$  represents the effect of feeding treatment.  $B_{\text{sex}}$  characterizes the effect of sex.  $B_{\text{nest}}$  symbolizes the effect of nest status..  $B_{\text{brood}}$  symbolizes the effect of brood status.  $\beta_{\text{loc\_num}}$  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*

A total of 26 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, Table 3.11, Table 3.11). 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 3.10). Males home ranges were 28% larger than female home ranges (Bayesian  $P$ -value = 0.99, Table 3.10, Table 3.12), and for every 6 locations included in home range estimates, home range size increased by 8% (Bayesian  $P$ -value = 0.86, Table 3.10).

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, Table 3.10, Table 3.11). Core use areas of nesting individuals and individuals that had broods were 126% and 73% smaller,

respectively, than individuals that were recorded with neither (Bayesian  $P$ -value = 1.00, 1.00, respectively, Table 3.10). Male core use areas were 8% larger than female core use areas (Bayesian  $P$ -value = 0.79, Table 3.10, Table 3.12). For every 6 locations included in core use area estimates, core use area size increased by 10% (Bayesian  $P$ -value = 0.92, Table 3.10).

### *Study 2: Feeder-fed Treatment vs Broadcast-fed Treatment*

A total of 35 bobwhite 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, Table 3.10, Table 3.11). Male home ranges were 39% larger than female home ranges (Bayesian  $P$ -value = 1.00, Table 3.10, Table 3.12). 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 3.10), or the locations included in home range estimation (Bayesian  $P$ -value = 0.70, Table 3.10).

Bobwhite core use areas were 26% smaller within the feeder-fed treatment than within the broadcast-fed treatment (Bayesian  $P$ -value = 0.95, Table 3.10, Table 3.11). Male home ranges were 28% larger than female home ranges (Bayesian  $P$ -value = 0.95, Table 3.10, Table 3.12), and nesting individuals had 36% smaller home ranges than those that had neither nested nor had a brood (Bayesian  $P$ -value = 0.78, Table 3.10). 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 3.10) or the number of locations included in home range estimation (Bayesian  $P$ -value = 0.58, Table 3.10).

Table 3.10. 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 3.11. Summary of Northern Bobwhite (*Colinus virginianus*) home ranges within each feeding treatment in years 2018 and 2019.

Year	Kernel %	Treatment	n	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 3.12. Summary of male and female Northern Bobwhite (*Colinus virginianus*) home ranges in years 2018 and 2019

Year	Kernel %	Sex	n	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