THE INFLUENCE OF HUNTING PRESSURE ON NORTHERN BOBWHITE (*COLINUS VIRGINIANUS)* BEHAVIOR

by

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(Under the Direction of JAMES A. MARTIN)

ABSTRACT

Understanding drivers behind behavior is essential for species management, for game species, this entails understanding the non-consumptive effects of hunting pressure. The Northern Bobwhite (*Colinus virginianus*) despite declining populations is intensively managed for in the Southeastern US. I conducted a study to investigate how bobwhites mitigate risk of hunters through direct behavioral mechanisms—evasive tactics, and an indirect mechanism—foraging behavior. Through a combination of behavioral observation, vegetation sampling, and intensive movement monitoring, I analyzed fine-scale behavior bobwhites on a private plantation in Georgetown County, South Carolina. I found that bobwhites altered their foraging strategy in response to hunters and that they used several factors when gauging risk during hunter encounters. With a better understanding of behavioral mechanisms we can better understand the complex hunter-covey interface and improve hunter satisfaction.

INDEX WORDS: *Colinus virginianus*, Behavior, Escape Behavior, Evasive tactic, First Passage Time, Foraging, Hunting Pressure, Northern Bobwhite, Movement Behavior, Perception, Risk, Risk Factors

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DEDICATION

I would like to dedicate this work to the people who inspired me to love and cherish the wilderness and work in conservation, my early mentors. Bill Wenk, for teaching me to love biology, but also to have fun with it. Jennifer Apple, who taught me the meaning of research and inspired me to pursue a career in ecology and to James Kernan, who taught me the beauty in fire-dependent ecosystems. Thank you for everything.

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TABLE OF CONTENTS

Page

CHAPTER

APPENDICES

LIST OF TABLES

Page

LIST OF FIGURES

Page

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION AND LITERATURE REVIEW

The importance of understanding non-consumptive (non-lethal) effects of hunting on game species is essential to understand drivers behind resource-use patterns. Predation pressure (including hunting pressure on game species) forces animals to make behavioral trade-offs such as modifying their activities to mitigate apparent risk (i.e., Kotler et al. 1991, Lone et al. 2014). These behavioral trade-offs can occur as a direct result of a predatory encounter (i.e., decisions relating to escape behavior) or can occur indirectly through modified behavior (i.e., foraging, habitat use, vigilance). If enough individual or inter-group variation exists between different strategies within a population, then these decisions could have an impact on individual survival (Southwood, 1988; Van Horne, 1983).

Hunting pressure directly impacts population demographics through mortality but also indirectly alters aspects of animal behavior such as movement patterns and habitat use (Little et al., 2015; Padié et al., 2015). Hunting pressure can create distinct selection forces for certain personality types as shy individuals have a tendency to encounter less hunters (Madden & Whiteside, 2013). Natural selection drives behavioral choices to optimize individual fitness (Lima & Dill, 1990), therefore making the non-consumptive effects of predation pressure equally important to the direct effects (i.e., mortality) for population dynamics (Davenport, Hossack, & Lowe, 2014). Predators can create fear and stress within their prey species, and this can cause anxiety and intimidation (Brown & Kotler, 2007; Preisser, Bolnick, & Benard, 2005). Spatial and temporal variation in predation risk may create difficult situations for prey species to accurately assess their risk level and creating a “landscape of fear” (Laundré, Hernández, & Altendorf, 2001).

Anti-predator behavior can result in indirect costs (i.e., time, energy, or lost opportunities) that are important to understand the cumulative effects of predation (Blumstein & Fernández-Juricic, 2010; Lima, 1998; White, Garrott, Hamlin, Cook, & Cunningham, 2011). Therefore in an attempt to mitigate risk but also maximize resources prey display threat-sensitive anti-predator behavior where the strength of the response correlates with the magnitude of threat perceived (Helfman, 1989). Further natural selection favors these individuals who are cognitively capable of assessing the degree of threat and responding accordingly (i.e., optimally; Sih 1980). The threat-sensitive predator avoidance hypothesis has received support over a wide range of taxa under a variety of anti-predatory behaviors such as modified foraging behavior or escape behavior (Martin, López, & Polo, 2009; Seamone, Blaine, & Higham, 2014; Turney & Godin, 2014; Wishingrad, Chivers, & Ferrari, 2014).

Foraging often puts prey animals in risky situations (i.e., increased exposure time, increased conspicuousness, or decreased attention); therefore, when food availability and predation risk overlap, prey species are forced to make trade-offs (Searle, Stokes, & Gordon, 2008). Under the starvation-predation hypothesis an animal’s foraging strategy must balance the risk of starvation with the risk of predation (Mcnamara, Houston, & Lima, 1994). In birds this trade-off is especially important because escape flight becomes increasingly difficult with excess weight. Foraging theory further predicts that under bouts of predation risk prey must either decrease their time spent foraging or increase their vigilance levels while foraging in order to compensate for predation threat (Kotler et al., 1991; Lima & Dill, 1990; Sih, 1980). But, due to the baseline level of fear established by predators simply being on the landscape, behavioral modifications would be predicted even when the predator is not physically present (Brown & Kotler, 2007; Creel & Christianson, 2008; Laundré et al., 2001).

Several theories explain how prey balance the trade-off between predation risk and foraging. Many of these theories feature the central premise that prey take advantage of variations in risk levels by foraging under less temporally risky times (Lima & Bednekoff, 1999) or less risky locations (Laundré et al., 2001). Considerations of variation in risk through space and time together can produce different inferences than if the two are studied in isolation (Creel & Christianson, 2008). Studies that test predictions of these hypotheses need to quantify received levels of predation and/or control background levels of predation, which can be a difficult task (Hebblewhite, Merrill, & Mcdonald, 2005). Field studies relating effects of predation pressure directly to foraging behavior have been few as foraging behavior is difficult to quantify and requires an exhaustive dataset (i.e., Freitas et al. 2008, Byrne and Chamberlain 2012). Some studies investigating this trade-off have used methods such as measuring giving up densities (GUD) and presenting predators in a controlled or monitored setting (i.e., Kotler et al. 2010, Wheeler and Hik 2014, Freeberg et al. 2016) but neither of these methods capture natural foraging patterns.

When faced with a direct encounter from a predator, prey face a myriad of decisions regarding escape including: what evasive tactic to use, when to initiate the evasive tactic and where to seek refuge (Cooper & Blumstein, 2015). These decisions have been modeled using optimality models and game theory in order to better understand and predict escape behavior in various scenarios (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Several factors are known to influence the apparent risk of predators including both endogenous (i.e., previous experience with predators) and exogenous factors (i.e., vegetation structure, distance to nearest refugia, predatory cues) and have been the key focus of research in this field (Stankowich & Blumstein, 2005). For example, the relationship between vegetation density and risk assessment is complicated as vegetation density affects the organism's ability to receive and interpret visual and auditory cues, and therefore could be considered obstructive (Devereux, Whittingham, Fernández-Juricic, Vickery, & Krebs, 2006; Metcalfe, 1984; Underwood, 1982). But vegetation density also serves as refugia and may be selected during risky times by cryptic prey species (Griesser & Nystrand, 2009; Lima & Dill, 1990; Turney & Godin, 2014). Studying the interaction between predation risk and the costs of fleeing (i.e., ecology of fear) allows insight into prey behavior and a better understanding of how we can manage prey species (Cromsigt et al., 2013).

Northern Bobwhites (*Colinus virginianus*; hereafter bobwhite) are adapted to capitalize on transient and dynamic resources and therefore may show diversity in resource use (Hovick et al., 2015; Southwood, 1988). Despite being one of the most studied game bird species, bobwhite populations continue to decline throughout most of its range (Brennan, 1991; Hernández, Brennan, DeMaso, Sands, & Wester, 2013). However, locally abundant populations of bobwhite persist on scattered private lands. These populations are supported through various intensive land management practices that mimic frequent disturbance regimes including prescribed burning, seasonal disking, and supplemental feeding (Greenfield, Chamberlain, & Burger, 2003; Gruchy & Harper, 2014; Madison, Barnes, & Sole, 2001; Osborne, Sparling, & Hopkins, 2012). On these private properties it is also possible to monitor individual exposure levels to hunting pressure as managers strictly dictate hunting regimes. Supplemental feeding, commonly applied on these private properties, of bobwhites creates direct spatial overlap of an abundant food source and predation risk as hunters often target these areas. In addition, bobwhites display multiple evasive tactics such as flushing, running through vegetation and holding (Stoddard, 1931) that vary in energy expenditure and therefore would be predicted to follow the threat-sensitive predator avoidance hypothesis (Helfman, 1989). For these reasons, the Northern Bobwhite is an ideal model system to study the influences of hunting pressure on aspects of behavior such as foraging and escape behavior.

This research is the first to simultaneously investigate the impacts of non-consumptive effects of hunting pressure on Northern Bobwhites in terms of foraging and willingness to tolerate risk. This study is the first to quantify foraging strategies of the Northern Bobwhite. Understanding the effects of hunting pressure on foraging activities can lead to decisions that can directly improve survival, habitat management, hunt success (detection of coveys), and hunter satisfaction. In addition, it is important to understand factors influencing risk perception and in turn escape behavior. Understanding behavioral responses of prey to hunting pressure can improve management suggestions for hunting regulations (Cromsigt et al., 2013). This research could also translate to an understanding of how bobwhites may respond to natural predators when presented with varying levels of risk. These two aspects of research will help to untangle the complex dynamics of risk perception and how behavioral choices influence resource selection strategies.

OBJECTIVES

The objectives of this study were to (1) investigate how bobwhites mitigate the risk of future encounters with hunters by modifying their foraging patterns and (2) investigate the influence of several factors on risk perception and escape behavior of Northern Bobwhites in response to hunter encounters.

THESIS FORMAT

This thesis is presented in manuscript format. Chapter 1 is a general introduction and broad literature review. Chapter 2 focuses on the effects of hunting pressure on Northern Bobwhite *(Colinus virginianus)* foraging behavior. Chapter 3 focuses on factors that influence risk perception and escape behavior of Northern Bobwhites *(Colinus virginianus)* in response to hunter encounters. Chapters 2 ad 3 will be submitted to peer-reviewed journals as indicated by the footnotes on the title pages. Chapter 4 is a general synthesis of findings and highlights directions of future research as well as pertinent management implications. Citations for the entire thesis follow the style of the peer-reviewed journal *Animal Behaviour*.

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CHAPTER 2

THE INFLUENCE OF HUNTING PRESSURE ON NORTHERN BOBWHITE FORAGING BEHAVIOR

McGrath, D.M., T.M. Terhune, J.M. Martin. To be submitted to *Applied Animal Behaviour Science*

INTRODUCTION

Prey species face a trade-off between resource acquisition and predation risk (Lima & Dill, 1990; Schoener, 1974). Optimal behavior theory's central premise is that prey optimize their fitness by balancing exposure to predators while maintaining energetic needs for survival and reproduction (Andrew Sih, 1980). Prey attempt to mitigate the risk of future encounters using behavioral shifts in foraging, habitat use, vigilance, or activity budgets (Creel, Winnie, Maxwell, Hamlim, & Creel, 2005; Embar, Raveh, Burns, & Kotler, 2014; Lima & Dill, 1990). The success of these decisions reflects the ability of an individual to optimize the costs and benefits (Kotler et al., 2010; Lima & Bednekoff, 1999).

How an organism responds to predation risk is directly related to its perception and interpretation of the encounter (Blumstein, 2003; Edgar, Paul, & Nicol, 2013). The threat-sensitivity hypothesis (Helfman, 1989) predicts that direct predator avoidance responses should vary by the perceived strength of the threat. Often this perception is the result of indirect cues, potentially associated with landscape attributes, rather than direct confrontation with a predator (Schmidt & Kuijper, 2015). Quantifying individual perception implies an understanding of the organisms' learning and memory processes which either could be spatial, related to specific events or attributes of, or a combination of both (Fagan et al., 2013). To evoke memory, an animal must accomplish two things, retention (storing the information) and retrieval (accessing the information). How long an animal retains certain information may reflect its overall importance or cognitive capabilities of the animal, or both (Fagan et al., 2013). In the context of hunting, animals are exposed to numerous cues that may be retained long-term such as exposure to a hunting dog, hunters, and firearms (Ciuti et al., 2012; Cromsigt et al., 2013).

Anti-predator behavior not only is driven by an individual's experience (i.e., endogenous factors), but exogenous factors (i.e., predator space use) can also dictate behavior (Mateo, 2007). Different hunting modes (i.e., stalking or cursorial) and different space use patterns by predators partially determine the optimal risk mitigation strategy by the prey species (Schmitz, 2008; Sih, Englund, & Wooster, 1998). Predator hunting mode and space use regulate where on a landscape a predator may prefer to hunt and therefore where prey are more likely to encounter them (Miller, Jhala, Jena, & Schmitz, 2015; Schmitz, 2008). Even when not physically present predators create fear for prey species (Brown, 1999) and prey could respond to spatiotemporal variation in this fear (Creel, Winnie, Christianson, & Liley, 2008; Laundré et al., 2001; Lima & Bednekoff, 1999). For game species, humans become an integrated part of this dynamic, as human pressures can exert equal or even greater risk than natural predators (Allendorf & Hard, 2009; Creel & Christianson, 2008; Darimont et al., 2009) and are rarely spatially (Bonnot et al., 2013; Lone et al., 2014) or temporally (Cromsigt et al., 2013) random. When making decisions about where to hunt, hunters bias their choice based on contextual factors, (e.g., density of other hunters) and past experience of success (Asmyhr, Willebrand, & Hörnell-Willebrand, 2013). This can create unique spatial patterns across the landscape (Asmyhr et al., 2013; Lone et al., 2014) that affect prey behavior. In addition, hunters also have to abide to strict regulations such as hunting seasons and permitted lands, further exacerbating the spatial and temporal mark they have on the landscape (Cromsigt et al., 2013).

Nonlethal effects of hunting game can cause significant impacts on behavior, particularly movement behavior, and therefore can have substantial impacts on population dynamics (Caro, 2005; Lima & Bednekoff, 1999), and in some cases may even be stronger than the direct, lethal effects of hunting especially when regulations set harvest limits (Cresswell & Quinn, 2013;

Stillfried, et al., 2015). Therefore, understanding the impacts of non-consumptive (nonlethal) effects of hunting is an integral, yet understudied, part of game species management (Kotler & Holt, 1989). A proper understanding of such effects can help managers improve resource management, hunting regulations, and factors relating to hunter satisfaction (Leopold, 1933; Stillfried et al., 2015). Therefore, I conducted a study to quantify the influences of risk from human hunters (accompanied with a pointing dog) on foraging behavior on the Northern Bobwhite (*Colinus virginianus*; hereafter, bobwhite).

The Northern Bobwhite, once abundant throughout its range, has been experiencing population declines since the 1920s (Brennan, 1991; Hernández et al., 2013; Stoddard, 1931). Due to its economic importance as a game species (Burger, Miller, & Southwick, 1999) managers invest significant time and effort on habitat management practices that improve resource acquisition, including prescribed burning (Brennan et al., 1998; Cram et al., 2000, seasonal disking (Greenfield et al., 2003; Madison et al., 2001), and supplemental feeding (Sisson 2000, Doerr and Silvy 2002, Haines et al. 2004). The practice of supplemental feeding has been shown to reduce home range size (Doerr & Silvy, 2002; Guthery et al., 2004; Haines, Hernandez, Henke, & Bingham, 2004; Sisson, Stribling, & Speake, 2000) suggesting that it reduces the space requirements needed to fulfill nutritional demands. However, these areas of supplemental food often become targeted areas for hunters, creating a direct spatial overlap of high food availability and high risk levels (Brennan et al., 1998; Burger et al., 1999). This spatial overlap creates an important nexus where bobwhites have to trade-off food and safety directly (Heithaus & Dill, 2002) and therefore a good model system to study the cost-benefit trade off of resource acquisition and predation risk.

Foraging behavior increases exposure levels to predators and requires a decrease in “safer” activities such as vigilance (Brown, 1999; Kotler et al., 2010). I expected bobwhites to respond to hunting pressure by modifying their foraging activities to decrease risk of future exposure (Casas, Mougeot, Viñuela, & Bretagnolle, 2009; Côte et al., 2014). I hypothesize that bobwhite mitigate future exposure to predation pressure following the same predictions of the threat-sensitivity hypothesis (Helfman, 1989) and that bobwhites may respond to variation in risk temporally (Lima & Bednekoff, 1999) or spatially (Laundré et al., 2001). Specifically, I predict that individuals under more frequent high risk situations, as imposed by hunters, will respond to risk by altering their foraging regimes in a compensatory fashion by—decreasing foraging bout duration and area but coupled with an increase in foraging bout frequency. Temporally I expected bobwhites to shift foraging bouts away from times of high hunting pressure (i.e., risky times; Lima and Bednekoff 1999, Creel et al. 2008). I also predict will spatially shift their foraging away from areas of high hunting pressure (i.e., risky space) despite high resource availability (Cresswell & Quinn, 2013; Laundré et al., 2001). I used several metrics to quantify ways bobwhites could be interpreting predation risk including different types of risk factors (i.e., distance to pointing dog or discharging a firearm upon flush). I also investigated the temporal effect of these risk factors—that is the effect on modifying foraging behavior may be a short-term response to recent risk exposures or could be a long-term cumulative response as a result of associated learning. I tested these competing hypotheses (Table 1) using intensive movement data indicating foraging behavior and quantified individual hunting experiences of Northern Bobwhite.

METHODS

Study Site

Research was conducted on private property in Georgetown County, South Carolina. The study area was approximately 1,957 ha comprised of about 52% loblolly pine *(Pinus taeda)* savanna (< 30 m basal area ha^{-1}), 11% longleaf pine *(Pinus palustris)* savanna (< 50 m basal area ha^{-1}), 10% bottomland hardwoods (e.g., mixed *Quercus spp. & Liquidamber styraciflua*), and 12% fallow fields. The remaining land cover was comprised of dove fields, duck impoundments, ponds, and plantation pine. In the pine savannas the understory vegetation consisted predominately of little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), big bluestem (*Andropogon gerardi*), blackberry (*Rubus fruticosus*), saltbush (*Baccharis halimifolia*) and wax myrtle (*Morella cerifera*). Common forbs on the site were small partridge pea (*Chamaecrista nictitans)* and ragweed (*Ambrosia artemisiifolia).* Soils were largely fine loam sands including Bladen, Wahee, Yauhannah, and Eulonia series (USDA 2006). The climate is considered subtropical and an average annual precipitation of 112 cm (US Climate Data 2016). Supplemental food was provided for bobwhites every 2 weeks via a spreader on a tractor along an 83.7 km trail (hereafter, feedline) systematically placed throughout the property at an approximate spacing of 200 m. This allowed for the feed to be spread throughout the vegetation without creating large concentrations of feed at the property-scale.

Field Methods

Bobwhite Trapping and Processing

I used baited (e.g., sorghum and cracked corn mixture) walk-in funnel traps (Stoddard, 1931) to capture bobwhites. Trapping occurred in October 2014 prior to hunting season. Traps were placed uniformly throughout the study area (to ensure interspersion of tagged individuals) at about 2 traps per acre and spaced 100 m apart in areas of dense cover. All individuals captured were marked with a unique number on an aluminum leg band (National Band & Tag Company) and sex, age (adult or juvenile), weight were recorded during processing. About 5 individuals per covey received Very High Frequency (VHF) radio transmitters (6.4 g radio tag; Holohil Systems Ltd), with only those individuals weighing over 132 g being selected for a tag to minimize possible radio handicapping (Palmer & Wellendorf, 2007; Terhune, Sisson, Grand, & Stribling, 2007). Transmitters were equipped with an activity signal that informed the observer if the bobwhite was actively moving. All trapping was conducted under SCDNR special use permit number G-14-04 and approved under TTRS IACUC permit number GB-2001-01.

Bobwhite movement and hunting monitoring

Bobwhites were tracked 3–5 times per week via homing telemetry (G. C. White & Garrott, 1990) and locations were recorded via an iPad equipped with a global positioning system (GPS). Telemetry was conducted on foot using signal strengths at several separate angles to determine an individuals’ location. An approximate location of the bird was taken at 15–30 m away from the observer (White & Garrott, 1990) to minimize observer impact. Telemetry error was measured using radio transmitters placed at known coordinates and was estimated at 12 m (n = 28, SD = 7.2) on average.

I used sequential telemetry to intensively monitor bobwhites and capture fine-scale movement patterns along daily movement tracks (see Byrne and Chamberlain (2012) for example). Sequential monitoring consisted of the same methods as stated above except the observer continuously tracked bobwhite coveys during the entire active period of bobwhites (approximately 20 min before sunrise to 20 min after sunset), taking locations at 30 min intervals. Sequential monitoring occurred systematically (about 3 times per covey) throughout the hunting season in order to capture variation in experience levels with hunters.

Bobwhites were monitored during all hunting events as scheduled by the property manager (*n* = 20). Hunting events on the property occurred via horseback and wagon, with 2–3 pointing dogs used at any given time. An observer followed the hunting party to record bobwhite encounter information, and location. The observer remained behind the hunting guide(s) at all times to ensure no directional bias in hunting based on observer telemetry. All bobwhite tracking occurred during 1st November– 1st March to capture the full duration of the South Carolina small game season.

Analysis Methods

First-Passage time analysis

I preformed first-passage time (FPT) analysis following the methods of Fauchald and Tveraa (2003) to determine area restricted search (ARS) behavior on bobwhite daily movement paths. Area restricted search behavior is characteristic of movement patterns expected to occur during foraging behavior, that is sharp turning angles and short step lengths (Byrne, Guthrie, Hardin, Collier, & Chamberlain, 2014; Oksanen, Niemi, Ahola, & Kunnasranta, 2015). First-passage time analysis uses a circle of a given radius, *r*, along the movement path and calculates the time spent by the animal inside the circle (Fauchald & Tveraa, 2003). Results of FPT analyses have been shown to be sensitive to track duration therefore only movement paths with >= 15 relocations were used for analysis (Oksanen et al., 2015; Pinaud, 2008). Along each movement path I interpolated locations at every 5 m and calculated FPT values for a range of circle radii of 10–100 m by increments of 10 m. I then calculated the radius at which mean (all paths) variance of log-transformed FPT peaked (20 m, Figure 2.1) to identify the proper search radius to use for analysis (Byrne & Chamberlain, 2012; Fauchald & Tveraa, 2003).

Classifying foraging behavior and determining foraging zones

First-passage time values are multimodal in distribution with modes being characterized by several peaks whereas ARS behavior is characterized by high FPT values (Lefebvre, Michaud, Lesage, & Berteaux, 2012; Oksanen et al., 2015). I used piecewise linear regression with a model selection approach to determine threshold values for ARS behavior for each movement path (Lefebvre et al., 2012). First Passage Time values were sorted into ascending order and fitted with a linear (reference), 1-, 2-, and 3-breakpoint models and compared using the Bayesian information criterion (BIC) value to select the best fit model for each movement track (Toms & Lesperance, 2003). Thresholds were based on the model with the lowest BIC and the greatest breakpoint FPT value (See Figure 2.2 for example). All selected thresholds were visually inspected using a histogram of FPT values to confirm that they made biological sense for that movement path (Oksanen et al., 2015). If the linear model was selected by the BIC method then no ARS behavior was said to occur for that movement track.

I defined a foraging bout as a consistent string of ARS activity with a minimum duration of 30 mins along a movement path. I segmented the FPT points into unique foraging bouts by grouping sequential locations above the ARS threshold. If points classified above the ARS threshold had a time difference > 1 hour, the foraging bouts were considered unique. I chose 1 hour as the time threshold because it translated roughly to 2 relocations and is approximately the time needed to digest a crop full of seed in poultry (Shires, Thompson, Turner, Kennedy, & Goh, 1987; Svihus, 2014; Vanderklis, Verstegen, & Dewit, 1990). Foraging bouts were then buffered by the search radius distance (20 m; Lefebvre et al. 2012) and any overlapping buffers were dissolved to create unique foraging bout polygons.

Variables of interest associated with foraging bouts included bout frequency, duration (min), area (ha), and bout timing (minutes away from 11:08 or 16:40) and spatial composition of risk. Bout timing was calculated to reflect the timing of foraging as compared to hours of peak hunting pressure. Hunting on my study site consisted of both morning and afternoon hunts creating two peak times of hunting pressure. I calculated mean times of both all morning and all afternoon hunts (11:08 and 16:40, respectively) and calculated the absolute time difference in minutes between hours of peak hunting and the start of a foraging bout to reflect bout timing compared to risky times (i.e., deviation from peak hunting). Daily movement variables were calculated for all movement parameters as the total of each parameter across all bouts that occurred within that day, with the exception of spatial composition of risk where the average was used (see below for details). All FPT analyses were performed using the adehabitatLT package (Calenge, 2006). Piecewise linear regressions were performed using the segmented package (Muggeo, 2008) and foraging bout zones were buffered in the rgeos package (Bivand & Rundel, 2011) in R 3.3.0.

Quantifying Hunting Pressure

Levels of hunting pressure were assigned to each individual movement track (and unique bout) based on both the cumulative and most recent encounters as noted from observations during hunts. The hunting pressure metric was assigned in three ways: number of times the specified covey was classified as being encountered by a dog or hunting party (Encounter) during all prior hunts, number of times a firearm discharged into the covey during all prior hunts (Shot), and the average Euclidian distance between bird point locations and dog GPS tracks

(Encounter Distance) across all hunts to reflect the cumulative interactions. The use of the distance metric was to ensure capture of information on encounters that occurred but may have been missed by research observers (i.e. if dogs failed to point). This distance metric represents proximity to a pointing dog from the bobwhite, thus, an increase in this metric represents a decrease in hunting pressure whereas the categorical variables represent a direct relationship. These variables were also calculated in the same fashion for the most recent hunting event metric except only the most recent hunting event was taken into consideration.

Quantifying Spatial Composition of Risk

In order to represent spatial variation in risk, I mapped hunting pressure across the landscape. I buffered all dog GPS tracks from each unique hunt by the error distance of the GPS unit (30 m; Garmin Astro 220). Then I converted each unique layer into a classified raster (i.e. hunted or not hunted). I then combined all raster layers so that each pixel value corresponded to the number of times it was considered hunted for all combined hunts (Figure 2.3). I divided this raster layer by the max number of times a pixel was hunted (7) to convert the map to a 0-1 frequency of hunted scale, with large values representing pixels that were more frequently hunted during the entire season (i.e., risky space). I overlaid all foraging bout polygons and calculated the mean value of this hunting metric for all pixels within that unique foraging polygon. For daily foraging variables, all unique bouts were averaged giving equal weight to each bout.

Foraging Models

Each foraging variable, with the exception of bout frequency, (Table 2.1) was modeled against a set of 10 candidate linear mixed effect models to investigate the relative influence of the hunting metrics (Table 2.2) on foraging behavior. Numeric covariates were scaled and centered to improve model convergence. All models included a random effect of bobwhite covey given movement in winter months is largely influenced by group dynamics (Williams, Lutz, & Applegate, 2003). For models incorporating a metric of the most recent hunting event, a second parameter, days since hunting event, was included in the models to control for variation in time between movement track data collection and hunting events. I included this term in the form of two candidate models, one with an interaction and one as a main effect. All models included a parameter, days into hunting season, in order to control for natural variation in foraging behavior due to seasonal effects. My null model included this parameter and the random effect of covey (hereafter, seasonal effects model). Where appropriate a log transformation was applied to the response variable to help normalize residuals. Bout frequency was modeled using the same procedures as described above but with a generalized linear mixed effect model with a Poisson distribution. Each model was matched with an *a priori* hypothesis and ranked with Akaike's Information Criterion for small sample sizes ($AIC_{c,}$ Burnham & Anderson, 2002) to determine which hypothesis had the highest amount of support from the data. We used a method of determining the marginal and conditional R^2 values for our models to assess model fit and help understand the variation explained by the fixed and random effects in our models (Table 2.3 & 2.4; Johnson, 2014; Nakagawa & Schielzeth, 2013).

RESULTS

Foraging and FPT summary

I collected a total of 514 daily movement tracks on 122 individual bobwhites for 30 unique coveys throughout October 2014–February 2015. First-passage time analysis identified foraging activity in 505 days (98%), 0–3 unique foraging bouts per day. Mean variance of log-transformed FPT peaked at 20 m, reflecting maximum variation in searching behavior of bobwhites at this scale (Figure 2.2). Mean number of relocations (non-interpolated) per movement path was 21 (SD = 2) and average path length was 464 m (SD=152).

Foraging bout duration was 169 min (mean, SD= 112) while total daily foraging duration was 249 min (mean, SD=115). Foraging bout area was 0.28 ha (mean, SD= 0.11) while total daily foraging area was 0.42 ha (mean, SD= 0.17). Bout initiation time was 11:24 (mean, SD= 2.2 hours) while bout frequency ranged from 1–3 with occurrence frequencies of 55%, 41%, and 3%, respectively.

Hypotheses Results

The most supported models, as indicated by AIC_c, differed at the bout and daily level, and to a lesser extent among foraging response variables (Table 2.2). At the bout level, recent encounter distance was the top supported model for both foraging duration and area ($w_i = 0.73$ and $w_i = 0.45$, respectively). At the bout level, the most supported model estimated that birds responded to hunting pressure with a 15.4 percent increase in foraging bout duration for every 114 m increase in encounter distance to a dog (decrease in hunting pressure) on the most recent prior hunt (Figure 2.4; $\beta = 0.154$, 85% CL = 0.107– 0.201). Similarly, at the bout level birds responded to hunting pressure with a 7.1 percent increase in foraging area for every 114 m increase in encounter distance (Figure 2.5; $\beta= 0.071$, 85% CL= 0.042– 0.099). These results support my predictions corresponding with H_1 (Table 2.1).

At the daily level, I found the most support for cumulative encounters influencing foraging duration ($w_i = 0.89$) and foraging area ($w_i = 0.80$). Recent encounter distance was my top supported model for influencing foraging bout frequency, ($w_i = 0.30$) but the cumulative encounter distance was also well supported ($w_i = 0.26$). At the daily level, bobwhites responded to being encountered once with an increase in total foraging duration by 43 minutes (Figure 2.6; 85% CL = 16.4–70.8) and to being encountered twice with an increase of 40 minutes (Figure 2.6; 85% CL = 13.4– 67.6), in contradiction to H_1 predictions (Table 2.1). Bobwhites responded to being encountered 3 or 4 times throughout the hunting season with a decrease in total forage area of 0.083 and 0.13 ha, respectively (Figure 2.7; 85% CL= 0.026– 0.14 & 0.02– 0.24) supporting H_1. I found a significant decrease in bout frequency, as my top model predicted a decrease in bout frequency of 1.083 (Figure 2.8; 85% CL= 1.020–1.15) for every increase in cumulative encounter distance of 101 m (decrease in pressure), supporting H_1 (Table 2.1).

I found limited support for H_2, as my top supported model for bout timing was the influence of the shot risk factor (w_i = 0.26); however, this model was only 0.39 ΔAICc units away from the null model (w_i = 0.23), therefore providing limited support. The top model for bout timing estimated a shift away from peak hunting hours by 33 min (Figure 2.9; 85% CL = 14.38– 52.28) when birds were exposed to a single gunshot, which does support predictions of H_2 as well as the threat-sensitivity hypothesis.

The top model for foraging bout spatial risk composition at the bout and daily level was the cumulative encounter model (w_i = 0.99 and 0.96, respectively). At the bout level, bobwhites used areas of higher hunting frequencies by 0.080 and 0.057 units (Figure 2.10; 85% CL= 0.038–0.121 and 0.0–0.113, respectively) after being encountered two or three times. However, after being encountered four times bobwhites used areas with lower hunting frequencies by -0.201 units (85% CL= -0.107– -0.296). At the daily level, bobwhites used areas with higher hunting probabilities 0.074 and 0.073 units of pressure (Figure 2.11; 85% CL= 0.030–0.118 & 0.0141–0.131, respectively) after being encountered two or three times. However, after being encountered four times bobwhites used areas with lower hunting frequencies by -0.217 units of hunting pressure (85% CL= -0.110– -0.325). These results contradict predictions of H_3 (Table 2.1) when bobwhites were encountered two or three times, but provide limited support for predictions of H_3 when bobwhites are encountered four times.

Post hoc we added an additional foraging variable, distance to supplemental feed, to better explain if the increase use of risky space was due to the correlation of risky space and supplemental feed and tested this variable against all candidate risk factors (Table 2.1). We saw a general trend of increase use of supplemental feed with increased exposure levels to hunters at both the bout and daily level (Figures 2.12 & 2.13). After bobwhites were encountered four times foraging bouts were 87.9 m closer to the feedline (Table 2.5, 85% CL= 64.0–111.8). At the daily level, bobwhites foraged 90.4 m closer to the feedline after being encountered 4 times (Table 2.5, 85% CL= 62.0–118.0).

Marginal R^2 values for our models ranged from 0.00–0.07 while conditional R^2 values ranged from 0.00–0.60 (Table 2.3 & 2.4). These values indicate a low explanation of variance provided by the models, however considering the data were field estimates of behavior this result was expected. In general, the top supported model by ΔAIC_c (Table 2.2) was also the model with the highest R^2 values (+/- 0.01 units, Table 2.3 & 2.4).

DISCUSSION

Taken collectively my results supported the compensatory foraging behavior hypothesis. Bobwhites responded to hunting pressure with decreased foraging duration and area but increased foraging bout frequency and an increase use of supplemental feed. I also found limited support for the risky times hypothesis, as bobwhites tended to shift away from times of high hunting pressure when they were previously exposed to firearms. However, I did not find equivocal support for the risky spaces hypothesis. Bobwhites responded to an increase in number of encounters with hunters through an increase use of risky space, until they were encountered four times. My results are the first to show bobwhites mitigate future risk of encounters with hunters via modifications to foraging strategies.

Time allocation between foraging and other competing activities is not just impacted during or immediately succeeding exposure to predation, but the effects of predation dictate future foraging behavior both in the form of a short-term response and a cumulative impact on behavior. This result corresponds to results found by Creel et al. (2005) who showed that elk *(Cervus elaphus)* displayed anti-predator responses to wolves *(Canis lupus)* even when they were not physically present on the landscape. Time allocation to competing activities such as anti-predator vigilance and foraging are tangentially affected by how efficient an animal is at foraging (i.e. feeding rate and food density; Baker et al. 2010, Powolny et al. 2014) and also level of predation risk the animal is exposed to (Brown, 1999). Theoretically how efficient an organism is at balancing this trade-off should impact their overall fitness (Pyke, Pulliam, & Charnov, 1977). Numerous studies have found that animals decrease foraging in favor of vigilance efforts when subjected to bouts of predation pressure (i.e., Baker et al. 2010, Ciuti et al. 2012, Powolny et al. 2014).

Models of foraging under predation risk often predict bimodal foraging behavior in order to balance the risk of predation with the risk of starvation (Mcnamara et al., 1994; Pravosudov & Lucas, 2001). This pattern suggests birds display two peaks in foraging activity, one early morning and one late day in order to replenish energy reserves (Mcnamara et al., 1994) while maintaining a period of inactivity between to limit exposure to predators. Another foraging study found evidence for a continuous foraging behavior in passerines (Bonter et al. 2013) but did not explicitly address predation risk, rather assuming constant background levels. My results indicated an increase in bout frequency (i.e., from 1-3 foraging bouts), but a decrease in duration and area, with increasing hunting pressure suggesting that as predation risk increased birds shifted their foraging patterns to a more bimodal or even tri-modal pattern but decreased the overall size and length of these foraging bouts to limit exposure levels. I posit two main reasons for this observed pattern in my study system. Bobwhites, unlike many bird species, possess a crop which allows for food storage—prolonging the need for subsequent intake of food and decreasing the need to forage as long. In addition, the permanent presence of supplemental feed possibly allowing bobwhites to increase feeding efficiency per unit time.

Prey often respond to temporal patterns in predation risk by focusing activities during less risky times (Lima & Bednekoff, 1999). Evidence for this pattern has been seen in nocturnal mammals limiting the amount of exposure time during periods of intense moonlight, when predators are known to be more active (P.C. Griffin,S.C. Griffin, Waroquiers, & Mills, 2005; Kotler et al., 2010). Bias in human behavior tends to create distinct temporal patterns in hunting (Asmyhr et al., 2013), a pattern I observed on my study site. I found a temporal shift in foraging bouts away from periods of high hunting pressure by about 30 minutes (Table 2.3) suggesting that bobwhites learned the temporal patterns of hunters and limited foraging activity around periods of high risk.

Prey have generalized anti-predator responses to loud or threatening stimuli to respond to novel situations (Frid & Dill, 2002). The report of a shotgun is one such stimulus due to its high volume and potential association with mortality of conspecifics. Several of my models identified exposure to shotguns as being significant stimuli to prompt anti-predator responses (Table 2.1 & 2.3). Anecdotally, I witnessed covey flushes to shotgun disengagement even when the hunting party was >500 m away, suggesting bobwhites learned the report of a shotgun as a threat (D.McGrath, personal observation). In a study of escape behavior in bobwhites Perkins et al. (2014) also noted that bobwhites showed a unique behavioral response to the report of a shotgun compared to other threat types. Other studies have shown noise sensitive responses to helicopter speed and volume in avian (McRoberts et al., 2011; Ward, Stehn, Erickson, & Derksen, 1999) and mammal (Goldstein et al., 2005) species that reflect this generalized anti-predator response.

In a study of elk *(Cervus elaphus)* and wolves *(Canis lupus)* in Yellowstone National Park Creel et al. (2008) also found evidence in support of the risky times hypothesis but a lack of support for the risky spaces hypothesis. My results agree with this finding as bobwhites continued to use areas exposed to higher levels of hunting pressure as hunting pressure increased throughout the season—until they were encountered four times (Table 2.3, Figure 2.3). It should be noted that on my study site hunting patterns were biased towards areas of supplemental feed as demonstrated by the overlap of high hunting frequencies and the feedline (Figure 2.3). Bobwhites foraging behavior was concentrated in areas of higher supplemental feed despite the increased risk of exposure to hunters. Doing so afforded them to potentially compensate for the decrease in duration and area of foraging bouts and improve foraging efficiency through increased food density. However, high hunter encounter rates (i.e., 4 encounters) forced bobwhites to forage in areas of lower risk suggesting that in my system there is trade-off between high risk and high energy supplemental feed.

I found a general trend of the temporal effect of hunting pressure depending on the scale of foraging behavior (i.e., bout and daily level). At the bout level, the recent exposure to hunting pressure influenced foraging behavior whereas cumulative hunting pressure were the most informative at the daily level. The results from the cumulative risk factors further supports the threat sensitive predator avoidance hypothesis as bobwhites behavioral response depended on the gradient of hunting pressure received throughout the season. This implies hunting pressure has short-term (i.e. few days after hunting event) effects on bobwhite foraging behavior as well as longer seasonal effects suggesting variation among the importance of the information to survival due to the differentiation in retention times (Fagan et al., 2013).

Relatively speaking I explored a low level of hunting pressure for bobwhites on privately hunted property (T.M. Terhune, personal communication). Nonetheless, I found empirical support for behavioral response to hunting in terms of foraging. Future research efforts should attempt to quantify hunting pressure across a wider gradient or with controlled levels of exposure. Research should also focus on other types of potential behavior shifts such as, resource use or vigilance in response to these exposure levels. Natural predators of bobwhites, such as Cooper’s hawks *(Accipiter cooperii)* and bobcats *(Lynx rufus)*, present a background level of predation pressure year-round (Rosene, 1969; Stoddard, 1931). Multiple predator threats may interact with each other and create conflicting patterns of risk. Few studies have quantified multiple predator effects on prey behavior (see Norum et al. 2015 for an expection) but efforts to understand how prey handle competing sources of risk should drive future research. A behavioral response to human hunting pressure has been documented in ungulate and mammal species spatially (Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015; Padié et al., 2015; Stillfried et al., 2015) and temporally (Little et al., 2015; Lone et al., 2015) but to my knowledge this is this first time a behavioral anti-predator response to hunting pressure has been shown in a game bird.

MANAGEMENT IMPLICATIONS

My results indicate that altering variation in hunting regime may reduce the amount of associated learning by bobwhites in response to hunting activity, thereby potentially increasing hunter satisfaction. Bobwhites altered their foraging behavior in response to encounters with hunters such that they reduced their foraging duration and restricted their foraging area. Therefore, we recommend that hunters maximize their spatial coverage and not limit their hunting efforts to the feedline for improved covey detection. Bobwhites also shifted their foraging times (away from traditional foraging times) in response to consistent hunter activity and encounters. As such, varying the timing and duration of hunting effort may improve hunting success and hunter satisfaction, especially late in the season. The use of GPS technology to track hunter and dog coverage can help to identify potentially under used areas. I also found that bobwhites used supplemental feed to compensate for decreased foraging duration and area. While its ethical considerations are beyond the scope of this work, provision of supplemental feed may be advantageous for bobwhite survival when it is evenly distributed throughout the property and not spatially concentrated.

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Table 2.1. Hypotheses and predictions for foraging response of Northern Bobwhites to hunting pressure on a private plantation in Georgetown County, South Carolina during the winter of 2014–2015.

Hypothesis	Applicable foraging variables	Time-based predictions	Space-based predictions
H_0: No response in foraging behavior to hunting pressure	All	None or seasonal effects (e.g., weather)	None or seasonal effects
H_1: Compensatory foraging behavior	Bout level: Duration, Area, Distance to feed Daily level: Duration, Area, Bout frequency, Distance to feed	Decrease in duration at both levels Increase in bout frequency Increase in use of feedline	Decrease in bout area at bout level
H_2: Risky times	Bout level: Bout timing Daily level: None	Deviation of foraging from peak hunting times	None
H_3: Risky spaces	Bout level: Spatial composition of risk Daily level: Spatial composition of risk	None	Decrease use areas of high hunting frequency within foraging zones

Table 2.2. Model selection results using ΔAIC_c values for all comparisons of candidate models of hunting pressure on foraging parameters of the Northern Bobwhite during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Risk factor indicates the variable of interest in the model. The temporal effect reflects if this variable was a cumulative metric spanning across the entire hunting season or if just the most recent encounter was observed. Bold values indicate models within 2 ΔAIC_c units of the top model for each response variable.

			Individual bouts					Daily				
Risk factor	Temporal effect	k	Duration	Area	Timing	Spatial risk	Distance To Feed	Duration	Area	Bout Freq	Spatial risk	Distance To Feed
Encounter Distance	Recent*	7	**1.97**	**0.00**	4.01	27.38	61.16	11.29	3.76	**2.00**	14.27	49.20
Encounter Distance	Recent	6	**0.00**	**0.26**	2.80	25.37	60.86	9.26	5.75	**0.00**	12.35	48.02
Encountered	Recent*	7	22.39	11.54	4.49	17.35	52.88	8.49	10.68	3.09	7.01	37.34
Encountered	Recent	6	20.58	9.58	2.72	18.31	51.00	6.45	9.80	3.44	9.87	35.80
Shot	Recent*	7	20.66	10.37	4.51	32.21	54.68	11.17	12.58	3.19	18.31	43.81
Shot	Recent	6	21.17	11.14	2.74	31.63	61.82	10.19	10.93	4.83	18.80	49.53
Encounter Distance	Cumulative	5	12.18	5.50	2.24	33.71	54.23	9.04	7.72	**0.29**	20.67	41.75
Encountered	Cumulative	8	20.91	3.22	**1.39**	**0.00**	**0.00**	**0.00**	**0.00**	7.64	**0.00**	**0.00**
Shot	Cumulative	7	21.84	7.68	**0.00**	32.84	35.48	10.79	12.88	7.64	22.92	17.31
Seasonal effects	NA	4	19.47	8.05	**0.39**	37.08	58.36	7.14	11.74	2.14	24.03	45.55

* Denotes an interaction term with risk factor and days after hunting event

Table 2.3. Model fit results using marginal and conditional R2 values for all comparisons of candidate models of hunting pressure on bout level foraging parameters of the Northern Bobwhite during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Risk factor indicates the variable of interest in the model. The temporal effect reflects if this variable was a cumulative metric spanning across the entire hunting season or if just the most recent encounter was observed. Bold values indicate the top supported model by ΔAICc in the candidate set.

Risk factor	Temporal effect	Duration		Area		Timing		Spatial risk		Distance To Feed	
		R^2M	R^2C	R^2M	R^2C	R^2M	R^2C	R^2M	R^2C	R^2M	R^2C
Encounter Distance	Recent*	0.05	0.20	**0.03**	**0.19**	0.02	0.10	0.04	0.38	0.01	0.53
Encounter Distance	Recent	**0.05**	**0.20**	0.02	0.20	0.02	0.09	0.04	0.38	0.01	0.54
Encountered	Recent*	0.01	0.14	0.01	0.16	0.02	0.09	0.06	0.41	0.02	0.58
Encountered	Recent	0.01	0.14	0.01	0.16	0.02	0.09	0.05	0.41	0.02	0.59
Shot	Recent*	0.01	0.14	0.01	0.17	0.02	0.10	0.03	0.40	0.02	0.54
Shot	Recent	0.01	0.13	0.00	0.16	0.02	0.10	0.03	0.41	0.00	0.54
Encounter Distance	Cumulative	0.03	0.17	0.02	0.18	0.02	0.09	0.03	0.41	0.02	0.55
Encountered	Cumulative	0.02	0.17	0.02	0.21	0.04	0.13	**0.07**	**0.46**	**0.07**	**0.60**
Shot	Cumulative	0.02	0.16	0.01	0.18	**0.04**	**0.12**	0.02	0.44	0.04	0.57
Seasonal effects	NA	0.00	0.12	0.00	0.16	0.02	0.09	0.01	0.42	0.00	0.54

Table 2.4. Model fit results using marginal (R^2M) and conditional (R^2C) R^2 values all comparisons of candidate models of hunting pressure on daily level foraging parameters of the Northern Bobwhite during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Risk factor indicates the variable of interest in the model. The temporal effect reflects if this variable was a cumulative metric spanning across the entire hunting season or if just the most recent encounter was observed. Bold values indicate the top supported model by ΔAIC_c in the candidate set.

Risk factor	Temporal effect	Duration		Area		Distance to Feed		Spatial risk		Bout Frequency
		R^2M	R^2C	R^2M	R^2C	R^2M	R^2C	R^2M	R^2C	R^2M
Encounter Distance	Recent*	0.01	0.11	0.04	0.27	0.01	0.58	0.05	0.44	0.01
Encounter Distance	Recent	0.01	0.11	0.03	0.26	0.01	0.59	0.05	0.44	0.01
Encountered	Recent*	0.01	0.11	0.02	0.22	0.03	0.64	0.07	0.46	0.01
Encountered	Recent	0.01	0.11	0.02	0.23	0.03	0.65	0.05	0.46	0.01
Shot	Recent*	0.01	0.13	0.02	0.24	0.01	0.59	0.04	0.44	0.01
Shot	Recent	0.00	0.10	0.02	0.25	0.00	0.59	0.03	0.46	0.00
Encounter Distance	Cumulative	0.00	0.10	0.03	0.29	0.03	0.60	0.03	0.47	**0.01**
Encountered	Cumulative	**0.04**	**0.19**	**0.04**	**0.30**	**0.07**	**0.66**	**0.06**	**0.51**	0.00
Shot	Cumulative	0.01	0.09	0.02	0.25	0.05	0.62	0.02	0.49	0.00
Seasonal effects	NA	0.00	0.09	0.00	0.24	0.00	0.59	0.01	0.47	0.00

Table 2.5. Estimates of effect sizes (β) from top models of hunting pressure influences on foraging variables of the Northern Bobwhite during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Models displayed were ranked at least < 2 ΔAIC_c than the null model. Bold coefficients represent effect sizes with 85% confidence limits that do not overlap zero and therefore interpreted to be biologically significant. Response variables that were transformed to standardize residuals are reported in transformed form.

Foraging Response	**Model Variables**	**β**	**SE**	**85% LCL**	**85% UCL**
Bout Level					
log(Duration)					
	Intercept	**4.918**	**0.056**	**4.837**	**4.998**
	Recent Encounter Distance	**0.154**	**0.033**	**0.107**	**0.201**
	Days since hunt	-0.038	0.033	-0.085	0.009
	Days into season	-0.006	0.028	-0.046	0.035
Bout Timing					
	Intercept	**323.341**	**8.661**	**310.869**	**335.813**
	Shot once	**33.332**	**13.157**	**14.386**	**52.279**
	Shot twice	21.949	19.207	-5.710	49.608
	Shot three times	31.235	25.248	-5.122	67.592
	Days into season	**-18.797**	**4.603**	**-25.426**	**-12.169**
log(Area)					
	Intercept	-0.407	0.029	-0.449	-0.365
	Recent Encounter Distance	**0.071**	**0.020**	**0.042**	**0.099**
	Days since hunt	0.011	0.017	-0.014	0.035
	Days into season	-0.010	0.015	-0.031	0.011
	Encounter Distance: Days since hunt	**0.031**	**0.021**	**0.002**	**0.061**
Spatial risk	**Intercept**	**0.254**	**0.031**	**0.210**	**0.298**
	1 Encounter	-0.044	0.030	-0.087	0.000
	2 Encounters	**0.080**	**0.029**	**0.038**	**0.121**
	3 Encounters	**0.057**	**0.039**	**0.000**	**0.113**
	4 Encounters	**-0.201**	**0.065**	**-0.296**	**-0.107**
	Days into season	0.006	0.009	-0.007	0.018
Distance to Feed	**Intercept**	**57.495**	**9.685**	**43.549**	**71.441**
	1 Encounter	2.29	7.858	-9.026	13.606
	2 Encounters	-0.376	7.41	-11.046	10.294
	3 Encounters	**-37.714**	**10.069**	**-52.213**	**-23.215**

	4 Encounters	**87.888**	**16.575**	**64.02**	**111.756**
	Days into season	**5.417**	**2.173**	**2.288**	**8.546**
Daily Level					
Duration	**Intercept**	**228.350**	**13.944**	**208.270**	**248.429**
	1 Encounter	**43.636**	**18.851**	**16.490**	**70.782**
	2 Encounters	**40.483**	**18.804**	**13.405**	**67.562**
	3 Encounters	-23.119	25.713	-60.146	13.908
	4 Encounters	-24.591	50.078	-96.704	47.522
	Days into Season	1.632	6.489	-7.713	10.977
Bout Frequency	**Intercept**	**0.384**	**0.037**	**0.331**	**0.437**
	Cumulative Encounter Distance	**-0.080**	**0.042**	**-0.141**	**-0.020**
	Days into Season	0.015	0.037	-0.039	0.069
Area	**Intercept**	**1.012**	**0.061**	**0.925**	**1.100**
	1 Encounter	0.095	0.075	-0.013	0.203
	2 Encounters	0.077	0.073	-0.029	0.182
	3 Encounters	**-0.205**	**0.099**	**-0.348**	**-0.063**
	4 Encounters	**-0.316**	**0.187**	**-0.586**	**-0.047**
	Days into season	**0.038**	**0.024**	**0.004**	**0.073**
Spatial Risk	**Intercept**	**0.247**	**0.031**	**0.202**	**0.292**
	1 Encounter	-0.027	0.032	-0.072	0.019
	2 Encounters	**0.074**	**0.030**	**0.030**	**0.118**
	3 Encounters	**0.073**	**0.041**	**0.0141**	**0.131**
	4 Encounters	**-0.217**	**0.075**	**-0.325**	**-0.110**
	Days into season	0.004	0.009	-0.009	0.018
Distance to Feed	**Intercept**	**58.996**	**10.115**	**44.43**	**73.562**
	1 Encounter	0.06	8.536	-12.232	12.352
	2 Encounters	-0.278	8.165	-12.036	11.48
	3 Encounters	**-41.141**	**10.855**	**-56.772**	**-25.51**
	4 Encounters	**90.411**	**19.704**	**62.037**	**118.785**
	Days into Season	**5.653**	**2.46**	**2.111**	**9.195**

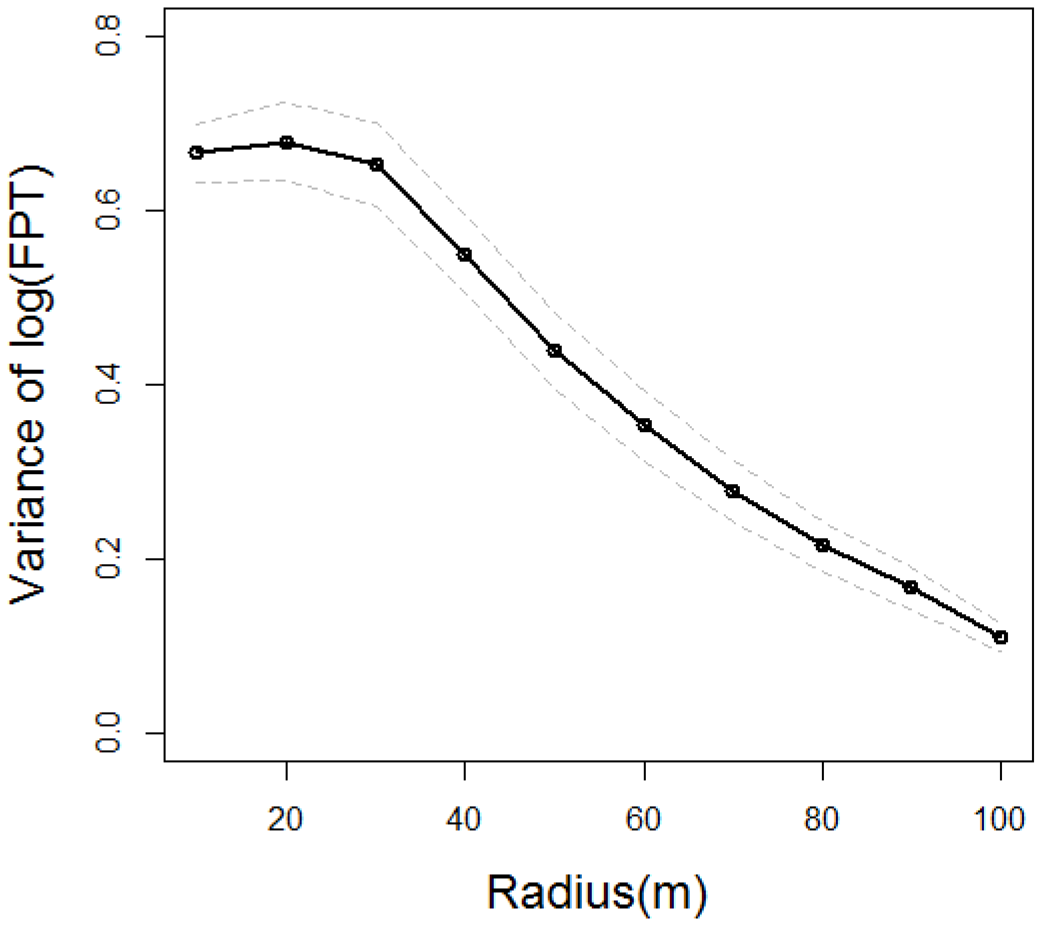

Figure 2.1. Mean variance (+/- SE) of log-transformed first-passage time values for 514 daily movement paths of 122 Northern Bobwhite as a function of circle radius collected during the winter of 2014–2015 in Georgetown County, South Carolina, USA. The peak variance occurs at 20 m, indicating the scale of area restricted search (ARS) behavior.

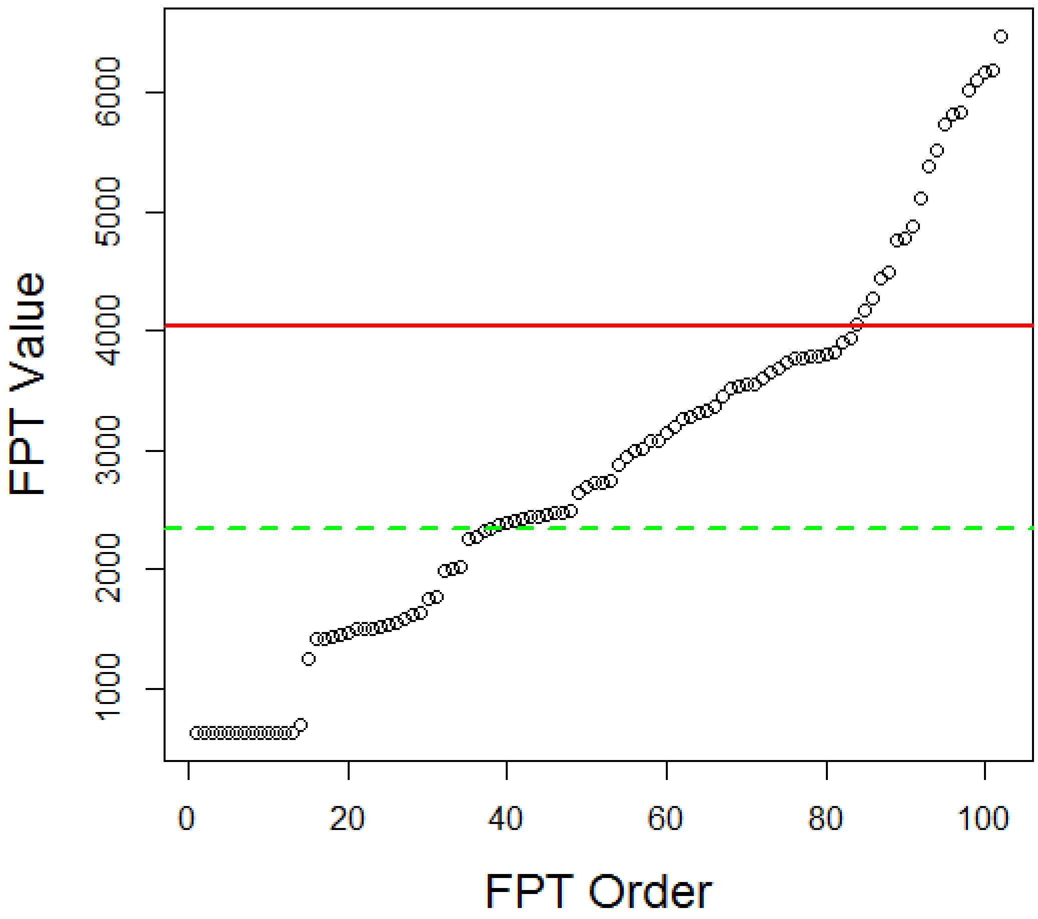

Figure 2.2. Example of piecewise linear regression used to select threshold values for movement tracks. All interpolated points ordered according to first passage time (FPT) value and fit with linear, 1-, 2-, and 3-breakpoint piecewise regression models. Bayesian Information Criterion (BIC) was then used to select the best model fit. In this example, BIC identified a 2-breakpoint model as the best fit with breakpoints at FPT values of 2334 (green dashed line) and 4035 (red line, selected as foraging threshold). All FPT values above 4035 for this movement track were considered points of foraging activity.

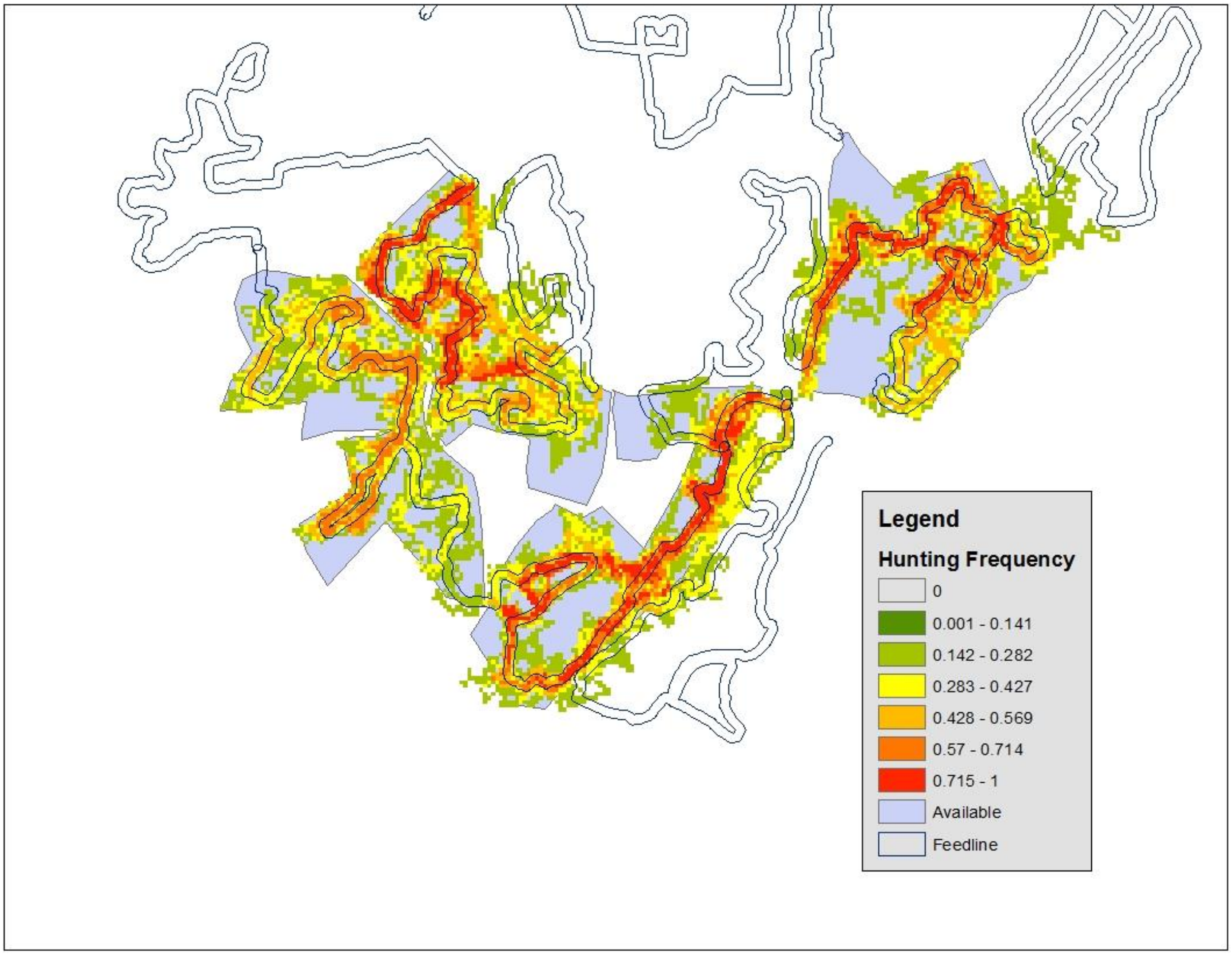

Figure 2.3. Cumulative hunting pressure map reflecting hunting patterns on our study site during the winter of 2014–2015. Times hunted represents how many times throughout the hunting season the location was covered by a scenting dog. Available areas were within the study area but never covered and have a hunting value of zero. For hunting frequency pixels were divided by the maximum number of times hunted (7).

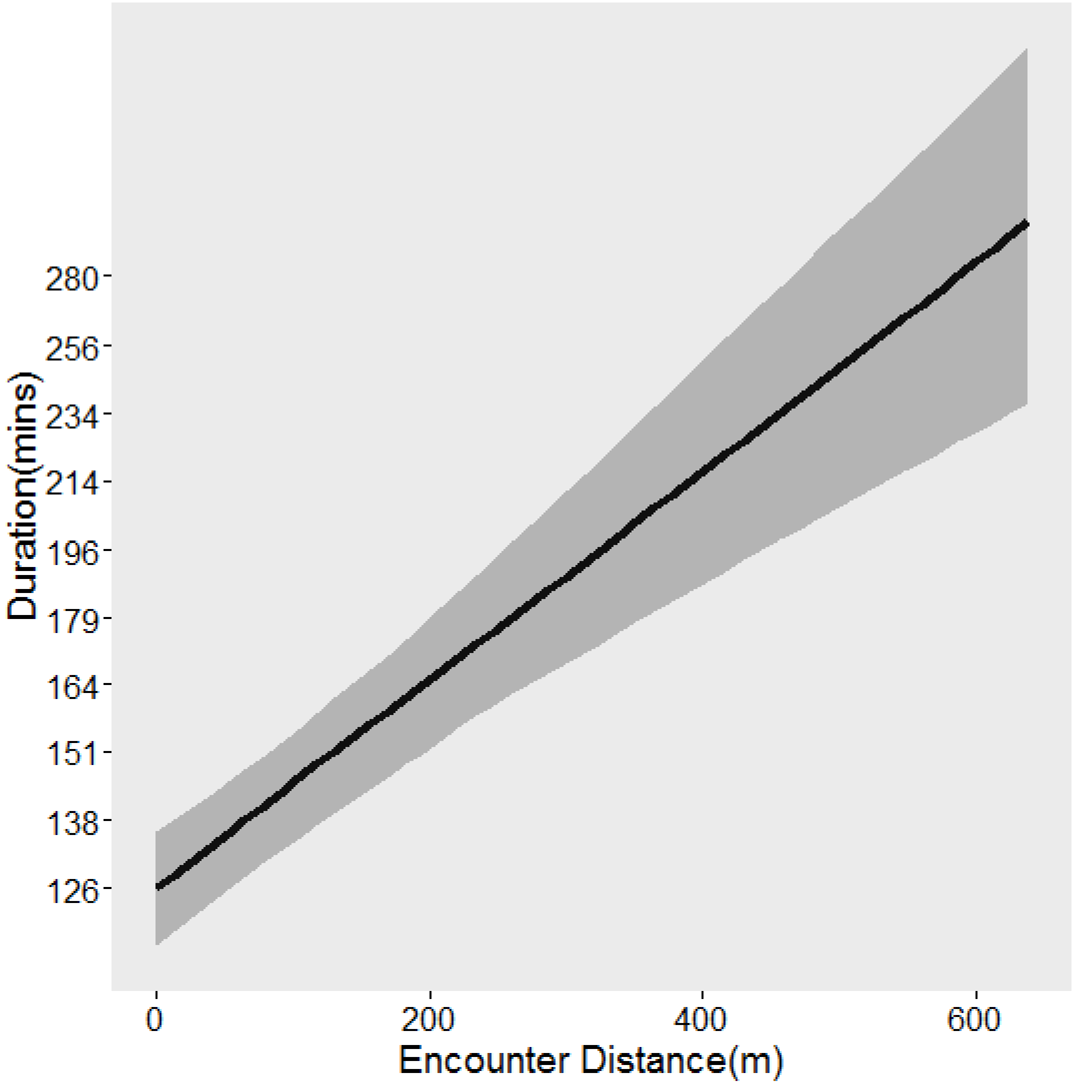

Figure 2.4. Effect of recent encounter distance with a pointing dog on Northern Bobwhite foraging bout duration, in minutes, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Gray ribbons represent 85% upper and lower confidence limits around the estimated effect size.

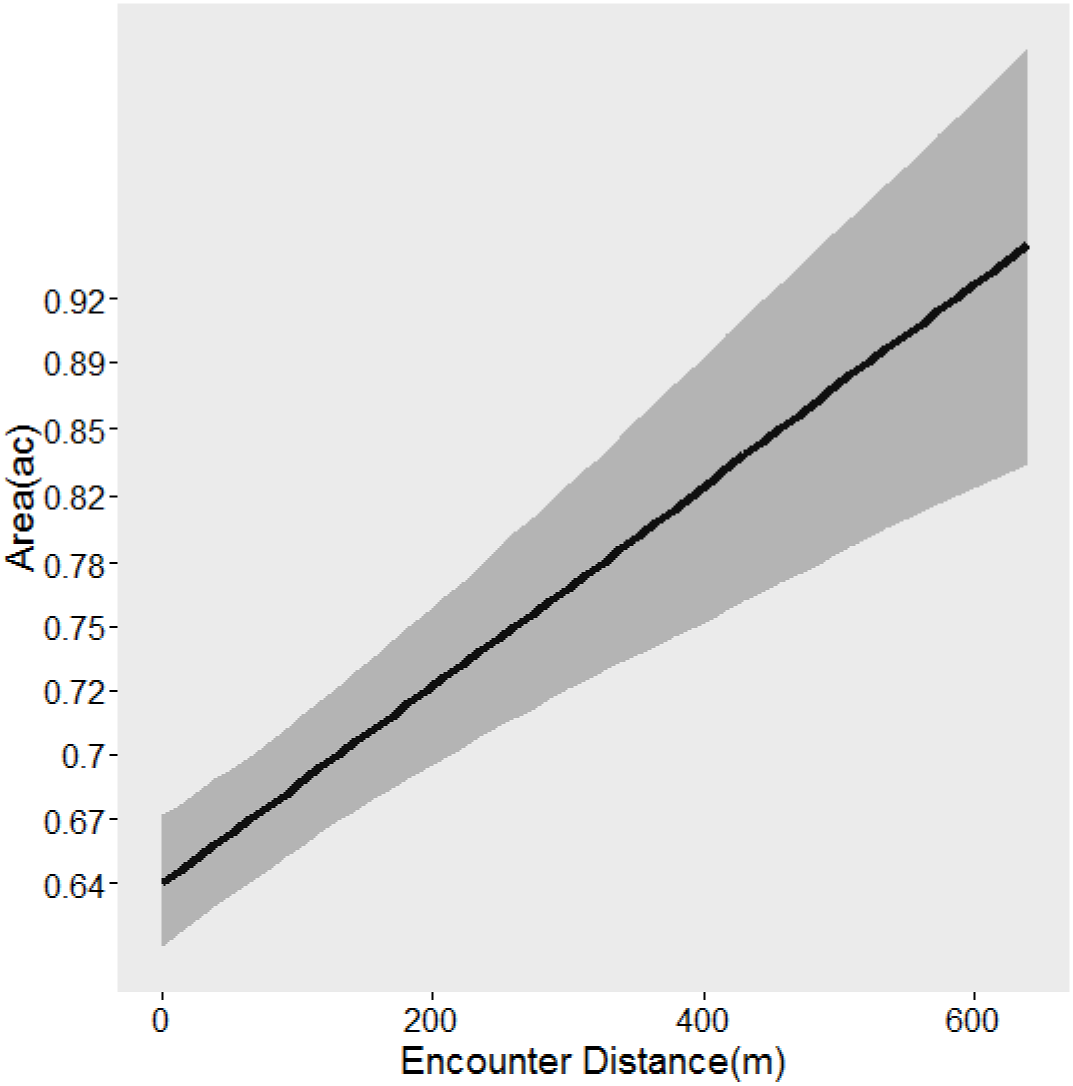

Figure 2.5. Effect of the most recent encounter distance with a pointing dog on Northern Bobwhite foraging bout area, in acres, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Gray ribbons represent 85% upper and lower confidence limits around the estimated effect size.

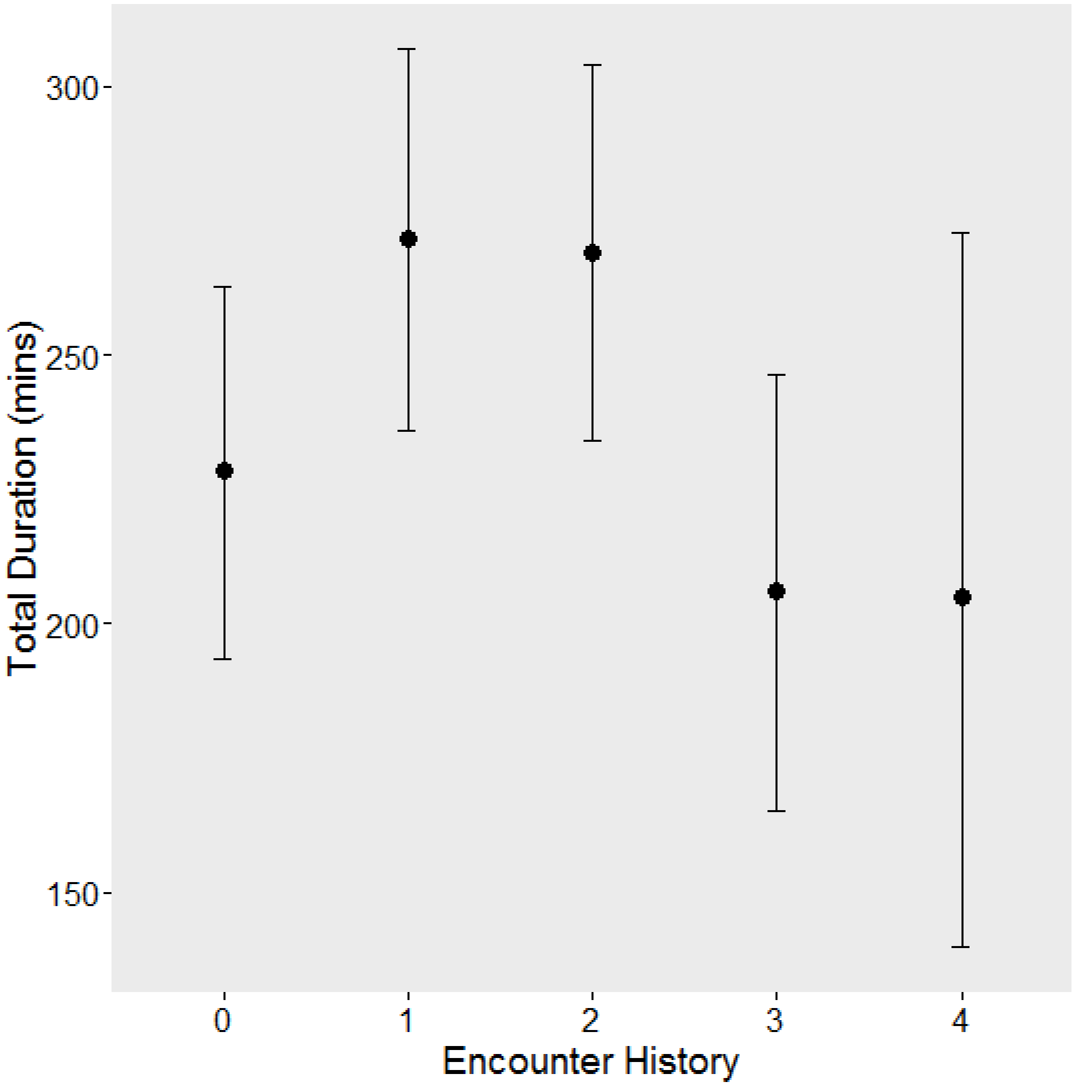

Figure 2.6. Effect of the cumulative encounter history to hunters on Northern Bobwhite total daily foraging duration, in minutes, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

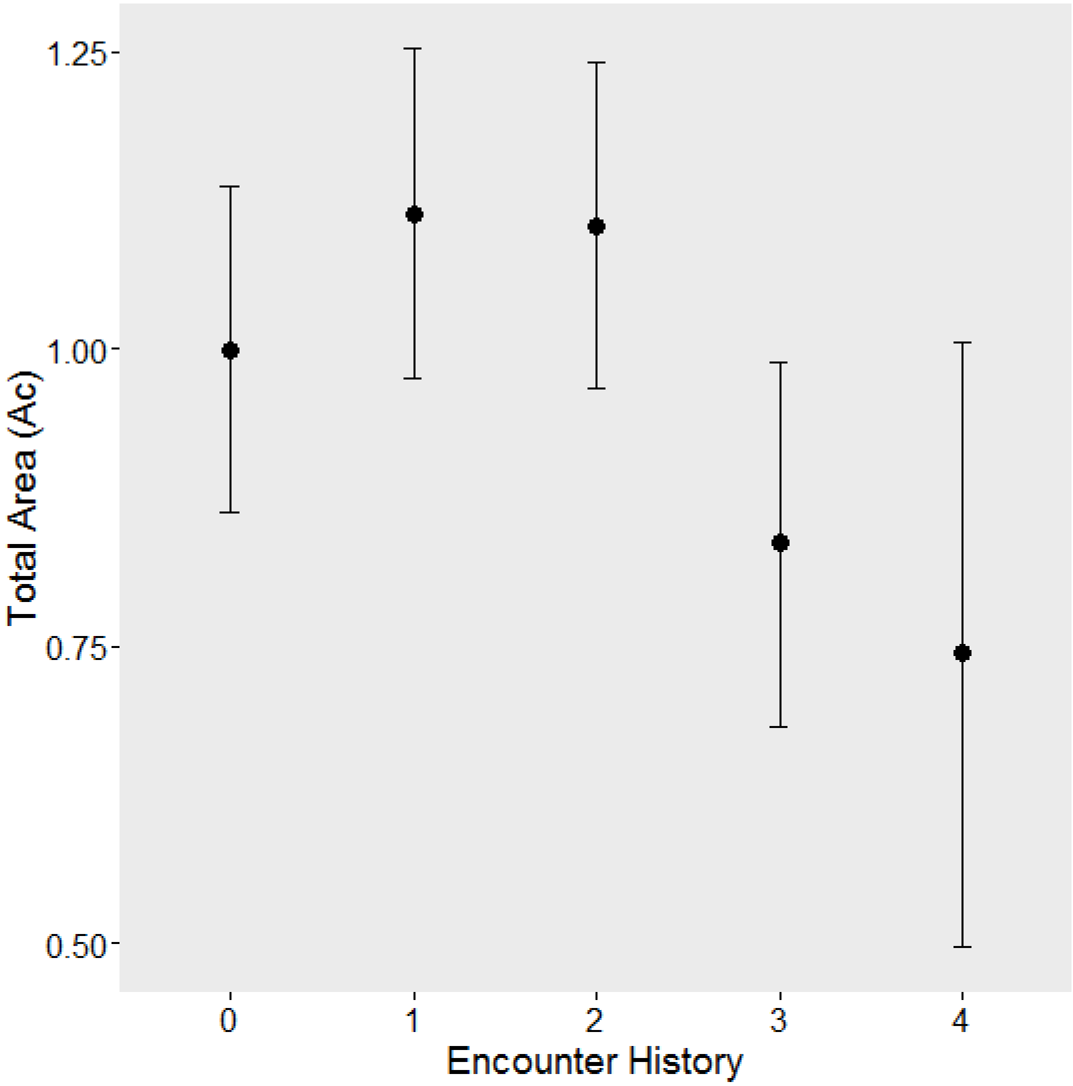

Figure 2.7. Effect of the cumulative encounter history to hunters on Northern Bobwhite total daily foraging area, in acres, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

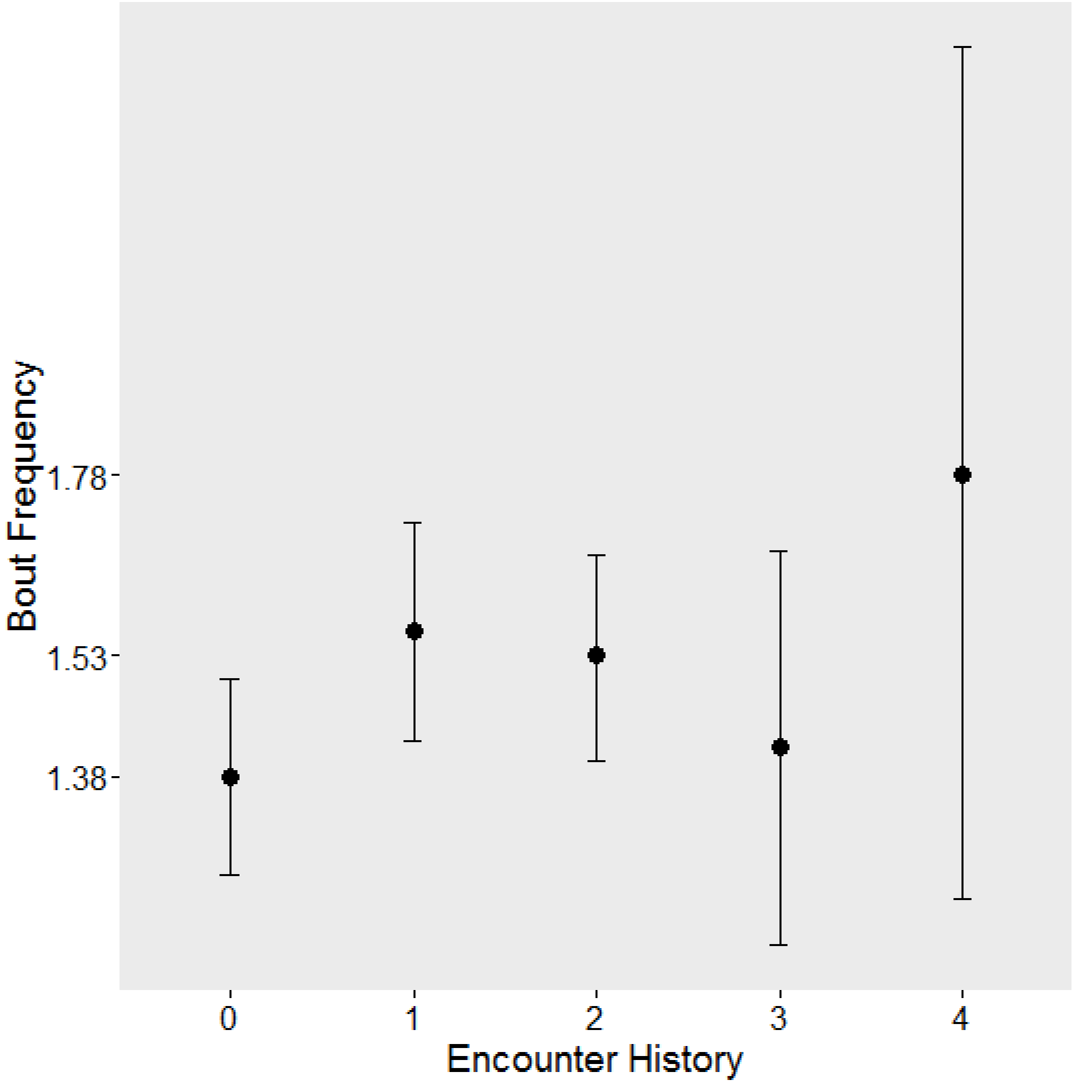

Figure 2.8. Effect of the cumulative encounter history to hunters on frequency of Northern Bobwhite foraging bouts, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

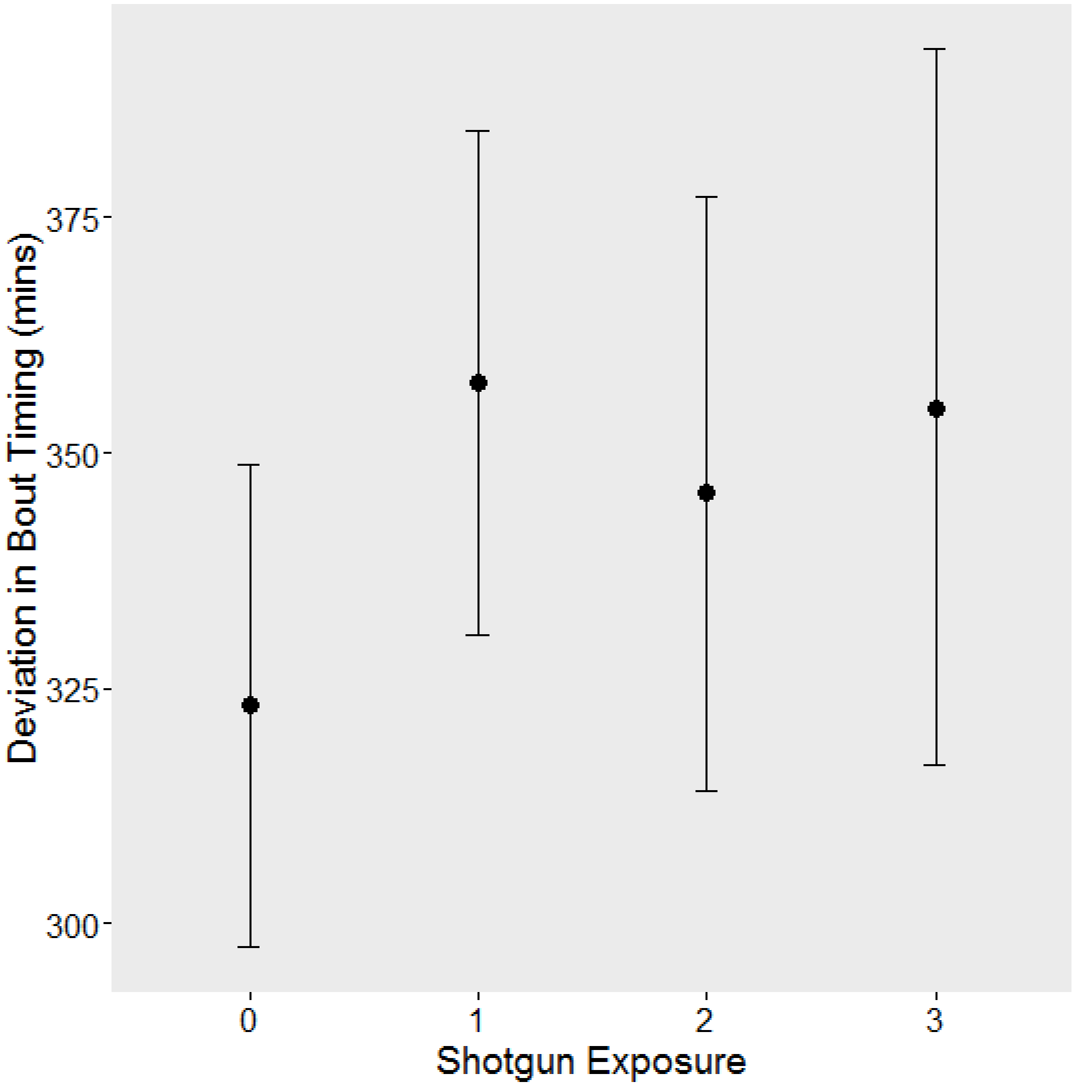

Figure 2.9. Effect of the cumulative exposure history to shotgun disengagement recent encounter on Northern Bobwhite foraging bout timing, in deviation from peak hunting times (11:00 or 16:40), during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

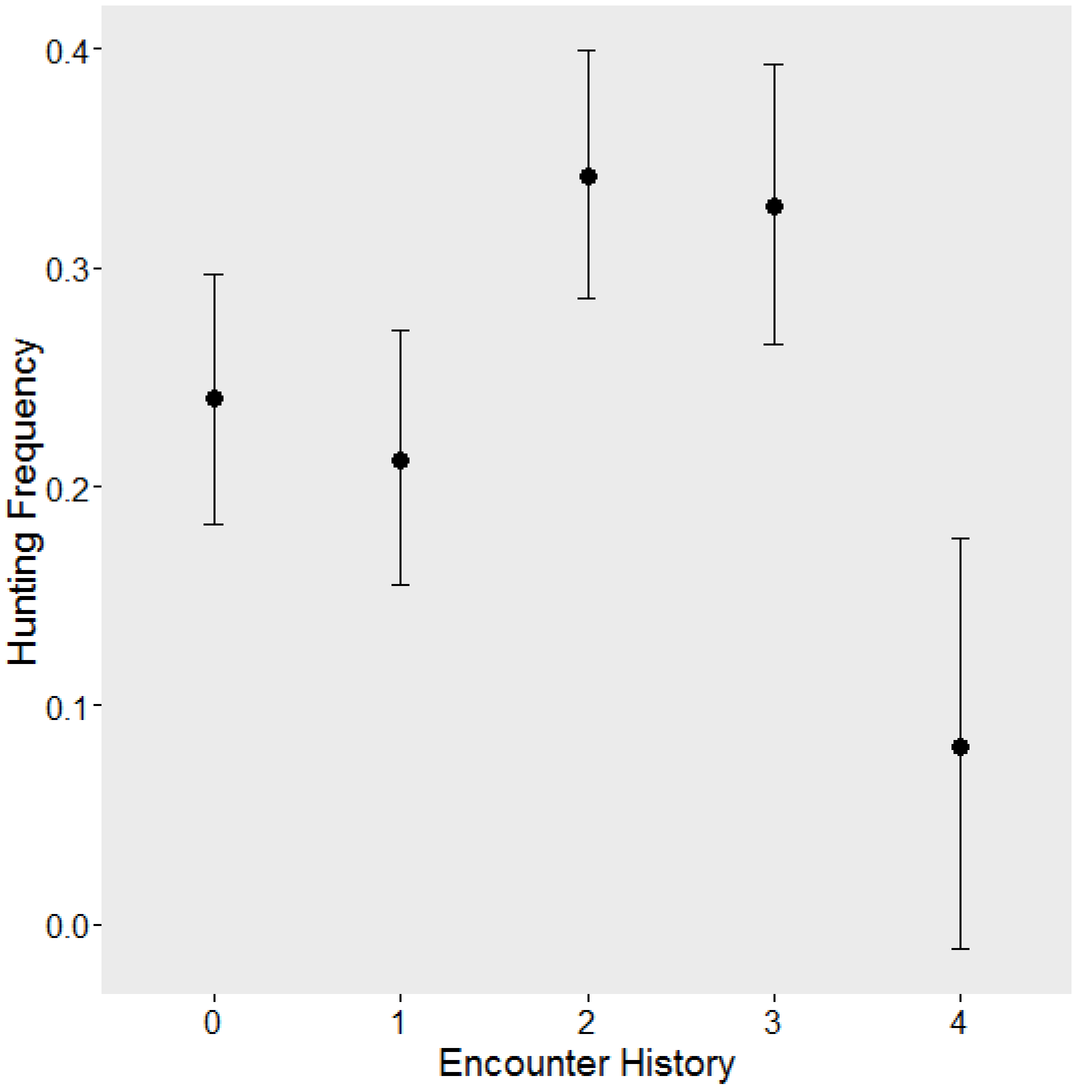

Figure 2.10. Effect of the cumulative encounter history to hunters on spatial composition of foraging bouts of Northern Bobwhites, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

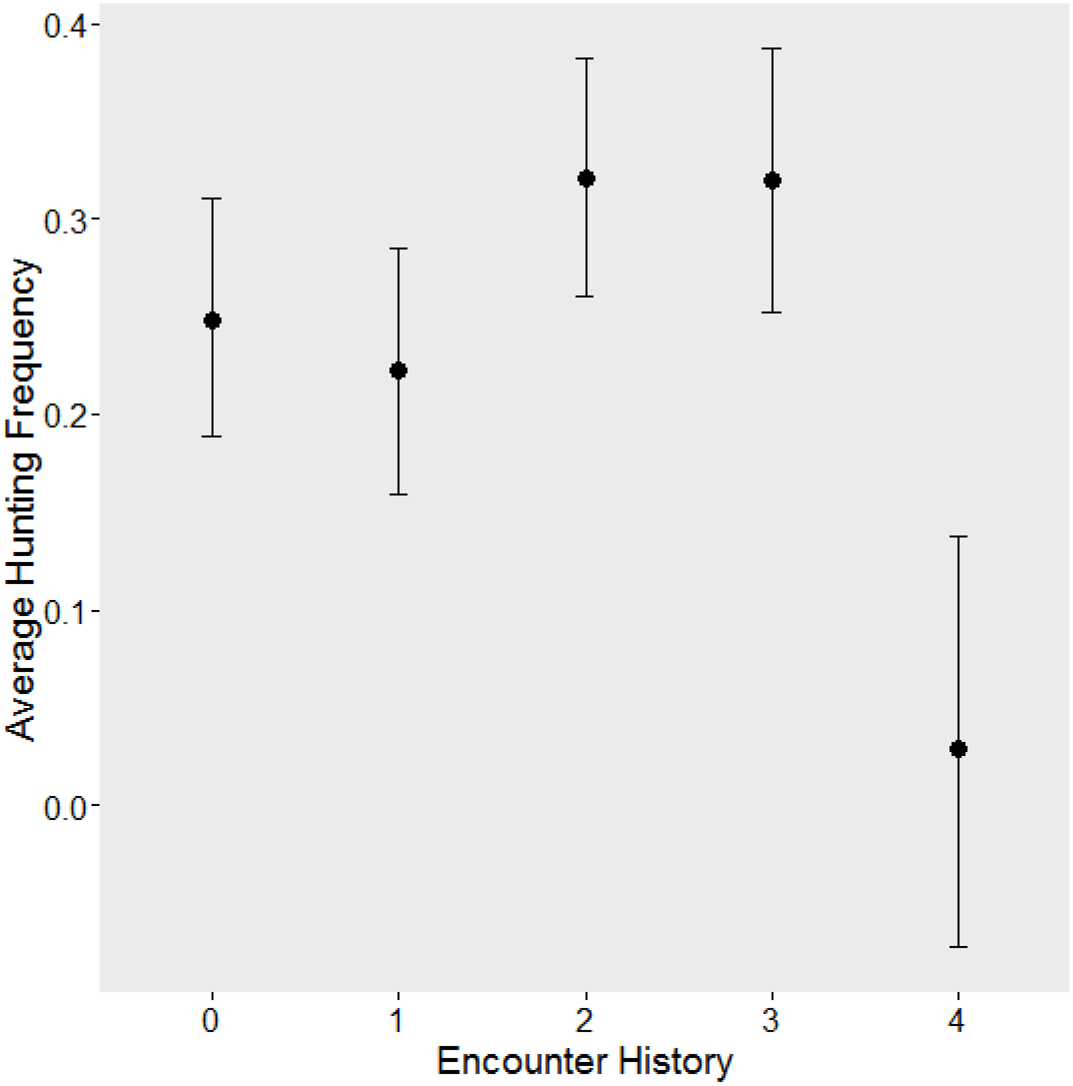

Figure 2.11. Effect of the cumulative encounter history to hunters on average daily spatial composition of foraging bouts of Northern Bobwhites, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

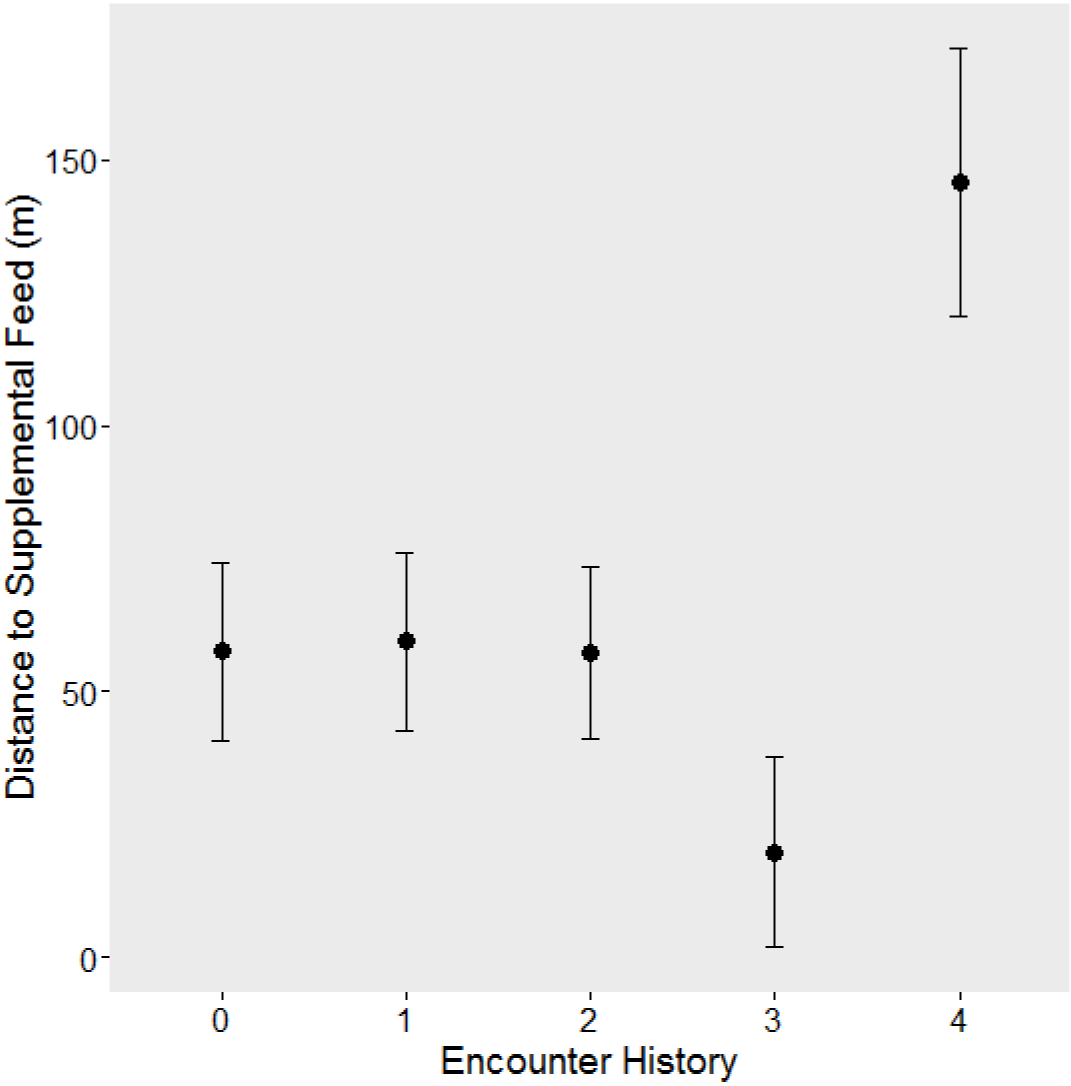

Figure 2.12. Effect of the cumulative encounter history to hunters on distance of Northern Bobwhite foraging bouts to supplemental feed, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

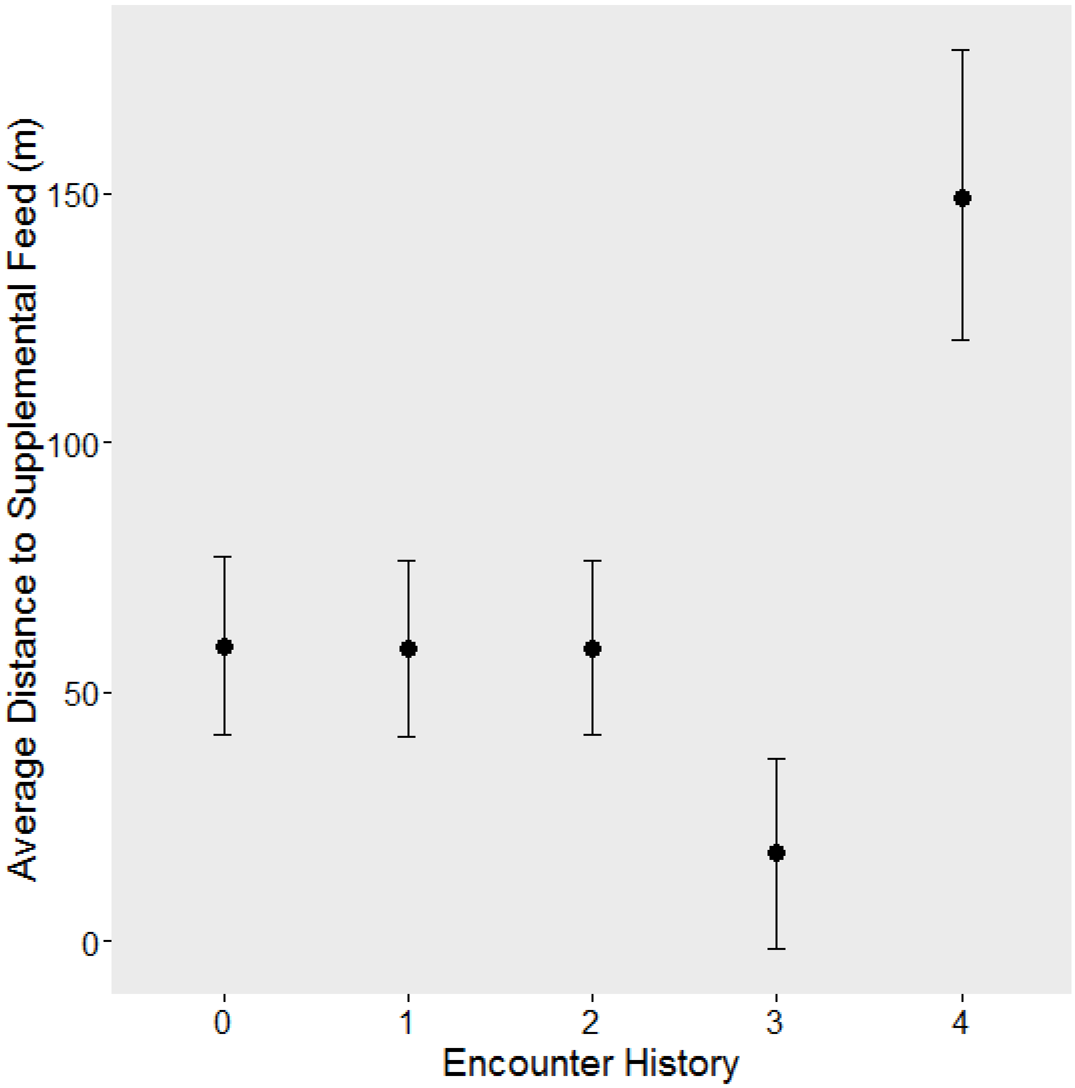

Figure 2.13. Effect of the cumulative encounter history to hunters on average daily distance of Northern Bobwhite foraging bouts to supplemental feed, during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Error bars represent 85% upper and lower confidence limits around the estimated effect size.

CHAPTER 3

BEHAVIORAL RESPONSE OF THE NORTHERN BOBWHITE (*COLINUS VIRGINIANUS)* TO HUMAN HUNTER INTERACTIONS

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INTRODUCTION

Predator interactions are strong evolutionary drivers on prey species and have resulted in a suite of anti-predatory behaviors to avoid such interactions by direct (fleeing or hiding) or indirect behaviors to reduce future encounters (i.e., altered foraging times). Upon a direct encounter with a predator, prey animals balance the cost of fleeing with the potential negative consequences of staying (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Costs of fleeing are missed opportunities to forage or engage in social activities (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). Costs also include physiological stressors or the energetic expenditure of the flight or escape locomotion (Cooper & Blumstein, 2014; Lima & Dill, 1990). Optimal escape theory attempts to model predictions of escape behavior (i.e., when to flee, how to flee, how far to flee) that optimize prey fitness under a given scenario (Cooper & Frederick, 2007; Cooper, 2009; Ydenberg & Dill, 1986).

Predictions of optimal escape models are dependent on how an organism evaluates risk (Blumstein 2003, Stankowich and Blumstein 2005) . Understanding the factors that influence risk perception is complex and includes habitat features such as vegetation structure (Wishingrad et al., 2014), food availability (Lima & Dill, 1990; Stears & Shrader, 2015), factors unique to individuals such as experience levels (Gregory, 2013; Martin et al., 2009; Mateo, 2007) or behavioral cues of the predators themselves (Cooper, 2011; Freeberg et al., 2016; Stankowich & Blumstein, 2005). These factors may be additive or interactive; yet research on escape behavior and multiple risk factors is sparse, especially under natural conditions, with a few exceptions (e.g., Devereux et al. 2006, Cooper 2009).

Dense vegetation structure can affect an animal’s ability to receive and interpret visual and auditory cues impeding predator detection (Devereux et al., 2006; Metcalfe, 1984; Underwood, 1982). In contrast, vegetation structure offers visual obstruction from predators and should be selected for in times of high risk by cryptic prey species (Griesser & Nystrand, 2009; Lima & Dill, 1990; Turney & Godin, 2014). Vegetation composition and structure vary among patches (Dawson, Carey, & Van’t Hof, 1992; Mark J Whittingham & Evans, 2004) creating spatial variation in predation risk that can vary among prey species depending on if it is perceived as visually obstructive or protective (Butler, Bradbury, & Whittingham, 2005; Caro, 2005; Whittingham & Evans, 2004). Despite its complexity, an understanding of how vegetation affects the perception of predation risk is necessary to understand how potential changes to habitat structure may impact perception of habitat quality by prey species (Wheeler & Hik, 2014; Whittingham, Devereux, Evans, & Bradbury, 2006; Whittingham & Evans, 2004).

Food availability affects escape behavior decisions as animals balance energy gains per unit time spent in the given habitat patch (Moody, Houston, & Mcnamara, 1996) with the cost of fleeing potential including giving up on a food resource or exposure to predators (Stears & Shrader, 2015;Whittingham et al., 2006). One such method of altering energetic gains associated with habitat quality is the process of supplemental feeding which directly increases food availability in a given habitat patch (Brown, 1999; Whittingham et al., 2006) and is a commonly used management practice for many game species (Buckley, Andes, Grisham, & Dabbert, 2015; Doerr & Silvy, 2002; Haines et al., 2004; Sisson et al., 2000). The presence of supplemental feed may increase the cost of fleeing and shift behaviors to those that maintain residence time or proximity (e.g., holding or running) to the concentrated food resource (Whittingham et al., 2006; Whittingham & Devereux, 2008).

Factors unique to predators such as size, orientation to prey, engaging behavior, or approach speed are cues used by prey species to indicate the intent of the predator (Cooper, 2011; Freeberg et al., 2016; Seamone et al., 2014). Proper distinction between threatening and non-threatening predator cues is important for prey species to make an accurate risk assessment regarding optimal escape decisions (Cooper & Blumstein, 2015; Lima & Bednekoff, 1999), as it would be energetically costly to implement escape strategies when not necessary. As such I would predict predatory cues such as posture and speed to affect escape decisions of prey by influencing their current risk assessment (Stankowich & Blumstein, 2005) and indeed several research studies have found significant influence of these factors under various contexts (Lee et al., 2013; Møller & Tryjanowski, 2014; Seamone et al., 2014).

Prior experience with predators is thought to directly influence risk perception as wariness increases the willingness of prey to flee in these future encounters (Gregory, 2013; Stankowich & Blumstein, 2005) and in game species the effect on anti-predator responses increases in strength throughout the duration of the hunting season (Casas et al., 2009). Hunting pressure may act as a unidirectional selection force as animals are likely to become more wary of humans with increased experience levels and select for behaviors that reduce encounters with hunters such as increased flight probability and an increase in vigilance levels (Bonnot et al., 2013; Casas et al., 2009; Côte et al., 2014).

I chose to investigate aspects of escape behavior as they relate to hunting (i.e., predator) interactions in a popular game species — Northern Bobwhite (*Colinus virginianus*; hereafter, bobwhite). Bobwhites display multiple escape behaviors including remaining hidden from predators (relying on crypsis), running through vegetation, and flushing upon approach (Rosene, 1969; Stoddard, 1931). These different tactics vary in energy expenditure and therefore under the threat-sensitive predator avoidance hypothesis would be predicted to be deployed corresponding with the intensity of threat perceived (Helfman, 1989). Perkins et al. (2014) examined bobwhite flight behavior in response to varying threat types, and found differences in flight distance in response to hunters and raptors. Yet to my knowledge, research examining the factors influencing the different behavioral tactics (i.e. holding, running, flushing) and associated response distances has not been conducted.

Flight initiation distance (hereafter, FID) defined as "the distance between a prey and an approaching predator when the prey begins to flee" (Cooper & Blumstein, 2015) has been used widely throughout the escape behavior literature as a proxy for quantifying prey escape decisions in terms of willingness to accept risk. Flight initiation distance can be generalized to apply to other escape related behaviors by modifying the definition to fit other response types such as ignoring or walking away from a predator by recording the distance between the prey and the predator at the time of response initiation (see Lee et al. 2013 for example). In essence, FID and other similar metrics capture the prey's decision on when to flee or initiate other behaviors and comparison of FID values in different scenarios allows for exploration of cues important to risk assessment (Blumstein, 2003). I used a method of direct observation of escape behaviors during bobwhite hunts using a multi-category classification because bobwhites exhibit multiple behaviors including remaining hidden (holding), flight (flushing), and run. I also quantified the response distance at which behavior initiation (hereafter referred to as RD) occurred for any interaction where pointing dogs came within "detectable range" of marked bobwhite coveys as a proxy for bobwhites' willingness to tolerate risk under any given scenario.

I hypothesized that bobwhite escape behavior is correlated to their level of threat perception (Helfman, 1989) and perception is driven by vegetation density, food availability, previous experience, and predator cues. Specifically, I predicted that bobwhites will perceive increased vegetation density as protective and therefore, cryptic holding behavior will be used compared to running or flushing. I also predicted that increased vegetation density would increase risk tolerance (i.e., decrease RD). In addition, I predicted higher food availability (proximity to supplemental food source) would raise the cost of fleeing for bobwhites. Therefore, I would predict an increase use of energetically costly escape behaviors (i.e., flushing) to be used and an increase in RD. I also predicted an individual's prior experience would increase high energy escape behaviors such as flushing and birds will be less willing to tolerate risk (i.e., increase RD). I predicted increased approach speed of a simulated predator (pointing dog) to induce more flushing behavior and expect bobwhites to tolerate less risk if the dog is actively moving (i.e., increase RD).

METHODS

Study Site

I conducted my research on a 2,000 ha private property located in Georgetown County, South Carolina. Land cover was dominated by loblolly pine *(Pinus taeda)* savanna (52%), longleaf (*Pinus Palustris)* pine savanna (11%), bottomland hardwoods (10%) and fallow fields (12%). The remaining land cover types consisted of a variety of man-made components such as dove fields, duck impoundments and ponds. The landscape received an intensive management regime of prescribed burning (50% of the property on a 1-year rotation), winter seasonal disking (fallow fields), and supplemental feeding on a systematically placed feed trail (sorghum spread throughout vegetation on 83.6 km trail every two weeks, hereafter referred to as the feedline). Common understory vegetation consisted typical early successional species such as; little bluestem (*Schizachyrium scoparium*), broomsedge (*Andropogon virginicus*), big bluestem (*Andropogon gerardi*), blackberry (*Rubus fruticosus*), saltbush (*Baccharis halimifolia*) and wax myrtle (*Morella cerifera*). Soils were mostly of the fine loam sand series, specifically Bladen, Wahee, Yauhannah, and Eulonia (USDA 2006).

Bobwhite Trapping and Processing

I used baited (e.g., sorghum and cracked corn mixture) funnel walk-in traps (Stoddard, 1931) to capture bobwhites. Trapping occurred before the start of hunting season (October) in 2013 and 2014. Traps were placed systematically throughout the study area (to ensure dispersion of tagged individuals) at about 2 traps per acre and spaced 100 m apart in areas of dense cover. All individuals captured were marked with a unique number on an aluminum leg band (National Band and Tag Co.) and individual sex, age (adult or juvenile based on primaries), and weight were recorded during processing. Approximately 5 individuals per captured covey received Very High Frequency (VHF) radio transmitters (6.4 g radio tag; Holohil Systems Ltd). Only those individuals weighing over 165 g were selected for a tag to minimize possible radio-handicapping(Palmer & Wellendorf, 2007; Terhune et al., 2007). Transmitters were equipped with an activity signal that informed the observer if the bobwhite was actively moving. All trapping was conducted under SCDNR permit number G-14-04 and all handling and processing followed guidelines approved by IACUC permit number GB-2001-01.

Bobwhite movement and hunting monitoring

Bobwhites were monitored via radio-telemetry (White & Garrott, 1990) during all hunting events. Hunting events on the property occurred via horseback and wagon, with 2–3 scenting dogs trained to “point” upon locating a covey. An observer followed behind the hunting party to ensure no observer induced impact on bobwhite behavior and recorded bobwhite encounter information, location, and bobwhite behavioral response. Telemetry transmitters were equipped with an activity signal that indicated whether the bobwhite was actively moving. The observer used a combination of direct visual observation, signal type, and signal strength to classify bobwhite escape behavior into holding, running, or flushing and mark the location of the birds at initiation of behavior. The observer remained behind the hunting guide(s) at all times to ensure no directional bias in hunting based on observer telemetry. All dogs wore Global Position System (GPS) units (Garmin Astro 220) to record movement paths during hunting events. Response distances (RD) were calculated in ArcGIS 10.2 (ESRI 2011) as the nearest Euclidian distance between marked bobwhite location and dog GPS track buffered by the unit error distance (30 m, Garmin Astro 220). All bobwhite tracking occurred during 1 November– 1 March during both years of my study (2013–2014 and 2014–2015). I measured observer telemetry error using radio transmitters placed at known coordinates and was estimated at 12 m (n = 28, SD = 7.2) on average.

Vegetation Sampling

After a hunting event, encounter locations were processed in ArcGIS 10.2 (ESRI 2011) to generate vegetation sample locations. In order to preserve encounters where detections may have occurred by bobwhites but failed to occur by pointing dogs, an encounter was classified as any bobwhite location to come within 30 m of the buffered dog GPS tracks from that specified hunt. I buffered encounter location by observer telemetry error (12 m) and randomly placed 3 point locations within the buffer. Several different metrics were used to describe the composition and visual obstruction properties of the vegetation. Composition metrics that were recorded included shrub cover (%), grass cover (%), forb cover (%), and bare ground (%) in a 1 m^2 Daubenmire frame (Coulloudon, Eshelman, & Gianola, 1999). In addition, a Nudds' board (Nudds, 1977) was used to measure vertical obstruction at 0.3 m increments above ground level (0–1.52 m). These metrics will be referred to throughout as visual obstruction readings (VOR). Vegetation metrics for each encounter location were averaged across the 3 subsamples.

Analysis Methods

General approach

I developed multiple sets of models to represent my hypotheses predicting the influence of vegetation structure, food availability, previous exposure to hunters, and predator approach speed (actively moving or pointed) on two aspects of escape behavior of bobwhites— the evasive tactic used and the response distance (RD) at which the tactic was employed. I used a model selection using ΔAIC_c (Burnham & Anderson, 2002) to explore relative support of my predictor variables on my two response variables. For RD models, model fit was also explored using marginal and conditional R^2 values to help understand the amount of variance explained by the fixed and random effects (Johnson, 2014; Nakagawa & Schielzeth, 2013).

Variables

My explanatory variables consisted of four sets of risk factors thought to influence decisions relating to escape behavior of bobwhites including metrics of food availability, vegetation density, previous exposure to hunters (number of encounters where a firearm was disengaged into the covey), and approach speed of the pointing dog (moving or pointed). Food availability was measured indirectly by calculating the Euclidian distance between the recorded encounter location and the feedline. Previous experience for bobwhite coveys was calculated from previous encounter information recorded from hunts. While I recognize that some adult birds may have previous experience with hunters if they lived through previous seasons, I measured experience levels beginning at zero at the start of each hunting season to solely reflect observed experiences. Response distance was measured as the Euclidian distance between the bobwhite covey and the pointing dog at behavior initiation, regardless of behavior type. This distance corresponded to the location of bobwhite covey and the location where the pointing dog held if a point occurred or the closest location the pointing dog came to the bobwhite covey if a point did not occur and was calculated using GPS and telemetry locations.

Multinomial escape models

I developed multinomial logit regression models in a Bayesian framework using the R package "MCMCglmm" v 2.17 (Hadfield, 2010). Using this package I was able to model the probability of each escape behavior occurring under multiple scenarios while allowing random variation due to covey identity via random intercepts (Gillies et al., 2006). All models were built to test my *a priori* hypotheses and compared using deviance information criteria (DIC; Spiegelhalter et al. 2002). I assessed biological significance of my variables using several summaries of the posterior distribution including the 85% highest posterior density (HPD) credible intervals derived from Markov Chain Monte Carlo (MCMC) estimations of the model coefficients and Btail; which is the fraction of the posterior distribution that overlaps zero on either side. Small values of Btail represent support for model coefficient estimates as they represent less overlap with zero (Lindenmayer et al., 2016). I assessed all models in comparison to a "null" model which included a seasonal covariate (days into the hunting season) and a random effect of covey. I ran models for 150,000 iterations with a burnin period of 50,000 iterations and a thinning interval of 10. I also visually inspected plots of my model coefficient estimates for parameter convergence. Multinomial logit regression models estimate the effect of factors on the probability (or likelihood) of observing one outcome as compared to a reference level. Holding was the most common behavior observed, thus I chose it as my reference response and as such all model coefficients are interpreted as a change in likelihood of one behavior compared to holding.

Response distance models

I also developed a series of *a priori* candidate models using linear mixed effects to model the effect of the covariates on RD. I assessed support for my hypotheses for this model set using a model selection approach using Akaike's information criteria for low sample sizes (AIC_c , Burnham and Anderson 2002) with models within <4 ΔAIC_c being considering competing hypotheses. I calculated 85% confidence limits around my beta estimates and considered parameters without confidence limits overlapping zero to be biologically significant. I used Pearson correlation tests to determine collinearity ($|r| > 0.7$) prior to modeling. Numeric covariates were standardized to have a mean of 0 and a standard deviation of 1 to improve model convergence and interpretability. In addition, I built a null model that consisted of a factor for behavior type days into the season (possible seasonal effects), and a random effect of covey (individual variation). All *a priori* hypotheses models contained these factors in addition to each factors evaluating the respective hypothesis.

RESULTS

General behavior

I observed Northern Bobwhite escape behavior on a total of 40 hunts during the hunting seasons of 2013–2014 and 2014–2015 ($n = 20$ and $n = 20$, respectively). I observed 97 total encounters with radio-tagged bobwhite coveys between pointing dogs and bobwhites. Dogs pointed 50 of those encounters (51%) and dogs did not point 47 of those encounters (49%). Of these encounters bobwhites were classified as holding 49 times (50%), flushing 27 times (28%) and running 21 times (22%). Of all encounters, hunters observed bobwhites during 57 (59%) encounters, discharging a shotgun into coveys during 30 of these encounters (31%). Running behavior had the largest RD, with an average of 2.85 m (mean, SD= 2.26), flushing RD being 1.45 m on average (mean, SD= 1.3) and holding having an RD of 1.93 m (mean, SD= 1.98).

Multinomial Behavior Models

I found support for two out of four of my *a priori* hypotheses that could influence evasive tactics of bobwhites (Table 3.1). My top supported model, as identified by ΔDIC, was the predator approach speed model (Table 3.1). According to this model, bobwhites were 1.17 times (Odds ratio, 85% HPD= 0.460–2.87; Btail=0.358) less likely to flush as compared hold and 3.56 times (Odds ratio, 85% HPD = 1.21–10.48; Btail=0.010) less likely to run as compared to hold. According to the predator approach speed model (Table 3.1), the likelihood of flushing as compared to holding while being pointed by a dog being 3.33 times less likely (Figure 3.1; Odds ratio, 85% HPD = 0.910–12.80; Btail = 0.033).

Effect sizes and directions were consistent among the three competing models for visual obstruction (Table 3.2), thus, I focus inference on the top VOR model. This model indicated that birds were 2.18 times less likely to flush as compared to hold (Odds ratio; 85% HPD = 1.29–3.59; Btail = 0.013) and were 2.70 less likely to run as compared to hold (Odds ratio; 85% HPD= 1.59–4.50; Btail= 0.004), similar to the top model. The model also indicated birds were 2.11 times less likely to flush as compared to hold for every ~13% increase in visual obstruction (Figure 3.2; Odds ratio; 85% HPD= 1.24–3.59; Btail = 0.015).

Marginal R^2 values for RD models ranged from 0.105–0.167 while conditional R^2 values ranged from 0.111–0.212 (Table 3.3). These values indicate a low explanation of variance provided by the models, however considering the data were field estimates of behavior this result was expected. In general, the top supported models by ΔAIC_c were also the models with the highest marginal R^2 values (Table 3.3).

Response Distance Models

I found support for three *a priori* hypotheses influencing response distance (Table 3.3). The top model (Table 3.3) indicated a positive effect of VOR at 0.3 m height above ground level on response distance with bobwhites increasing their RD by 0.55 m (Figure 3.3; $\beta = 0.55$; 85% CL = 0.26–0.85) for every 17.3% increase in VOR. Similarly, I found that bobwhites increased their RD by 0.36 m (β; 85% CL = 0.08– 0.66) for every 13.1% increase in VOR at 0.61 m from ground height (Table 3.4) but this model was less supported ($\Delta AICc = 3.8$). These results contradict my prediction that vegetation density would be perceived as protective by bobwhites. The predator approach speed model (Table 3.3) indicated that bobwhites decreased their RD by 0.73 m ($\beta = -0.73$; 85% CL = -1.27– -0.19) when pointed by a pointing dog as compared to when the pointing dog was moving. The previous exposure to shotguns model (Table 3.3) indicated support of my hypothesis on prior experience influencing RD (Table 3.3). The model indicated that bobwhites increased their RD by 0.55 m for every additional time they were shot at previously (Figure 3.4; $\beta = 0.55$; 85% CL = 0.16–0.94).

DISCUSSION

My study was the first to simultaneously investigate factors that influence evasive tactics and willingness to accept risk of the Northern Bobwhite in response to hunters. My results showed that bobwhites use several key factors when evaluating risk during bobwhite-hunter interactions including predator approach speed, vegetation density at various heights, and previous experience. I found these factors influenced two aspects of escape behavior— the choice of evasive tactic (i.e., holding, running or flushing) and when to employ that tactic (i.e., RD). Taken collectively these results indicate that bobwhites use contextual factors and prior experience to assess risk during interactions with scenting dogs and human hunters.

My results indicate that bobwhites gauge approach speed of a ground predator to inform escape behavior—that is when a pointing dog was actively moving, bobwhites were less willing to tolerate risk (Table 3.2 & 3.4). Studies that have examined prey responsiveness to predator approach speed in lizards (Cooper, 2011) and sharks (Seamone et al., 2014) have found similar results. In a study of avian escape responses to oncoming vehicles DeVault et al. (2015) showed that captive brown-headed cowbirds *(Molothrus ater)* were sensitive to vehicle speed suggesting the cue is important in assessing risk tolerance. They also found evidence for ineffective risk assessment at extremely high speeds (well above a natural predator's capability), suggesting that there may be evolutionary constraints on this mechanism. Anecdotally, I observed that the orientation of the pointing dog’s head was often, but not always, facing the direction of the bobwhite covey upon detection (D. McGrath, personal observation). While I did not quantify it in this study, this signal is likely another important predator cue bobwhites use when assessing predator intent (Camp, Rachlow, Woods, Johnson, & Shipley, 2012; Freeberg et al., 2016; Seamone et al., 2014) and could be contributing to some variation in escape behavior. Optimal escape strategy is highly dependent on predator hunting mode (i.e., aerial vs. stalking) and therefore prey should respond to these variations (Sih, 1980). Yet accomplishing this is a difficult task when prey are simultaneously exposed to multiple sources of risk (Atwood, Gese, & Kunkel, 2009). Potts (2012) noted that partridge species (*Perdix spp.)* respond to ground threats by flushing and to aerial threats by remaining hidden in cover. This balance of strategies would limit the amount of visual exposure of the prey to predator in both scenarios. In bobwhites, differences in escape behavior to threat type have been noted between raptors (aerial) and hunters (ground; Perkins et al. 2014). Differential interpretation of these predator cues may be imperative to successful escape behavior and therefore survival (Sih et al., 1998).

Prior exposure to hunters (when shotguns were discharged) made bobwhites warier in future encounters (i.e. increase RD & increase in flushing; Table 3.2 & 3.4). This result also supports numerous accounts of bobwhite hunters that state birds are more likely to get “wild” throughout the hunting season (Stoddard, 1931) and could partially explain why harvest rates tend to decline as the hunting season progresses (Cromsigt et al., 2013). The effect of repetitive exposure to predators has also been shown to impact wariness in several other hunted species (Côte et al., 2014; Little et al., 2015). Interestingly, I did not see this response in escape behavior when prior exposure to hunters did not involve a firearm being discharged. This suggests that bobwhites show threat-sensitive predator avoidance responses (Helfman, 1989) and can respond to changes in perceived threat levels. Perkins et al. (2014) also found a unique behavioral response to shotguns and suggested that it was the report of the gun which triggered the response. This logic agrees with my findings and other studies that have found loud noise (i.e., helicopter volume) to elicit escape behavior as it is considered a general threatening stimuli (Frid & Dill, 2002; Goldstein et al., 2005; McRoberts et al., 2011).

My top VOR models between model sets (Table 3.1 & 3.3) reflect different patterns on how bobwhites may be interpreting cover in terms of escape behavior. At low heights (0.30 & 0.60 m) dense vegetation increased RD (Table 3.4) suggesting it lowers risk tolerance. Vegetation density at this height would decrease the ability of bobwhites to see, making them more reliant on non-visual cues. Other studies of ground foraging birds have found similar effects of low height vegetation density on escape behavior (i.e., Butler and Gillings 2004, Whittingham and Evans 2004). Whittingham et al. (2004) showed that despite an increase in vigilance levels, chaffinches *(Fringilla coelebs)* were 24% less efficient in detecting predators in dense stubble fields therefore showing dense vegetation is obstructive to predator detection and may explain increases in wariness behavior.

Contrary to the previous result, bobwhites were less likely to employ high energy behaviors (i.e., flushing) in areas with increasing vegetation density at 0.60, 1.0, and 1.30 m (Table 3.2) favoring cryptic behavior (holding) under these conditions. This suggests that risk was perceived to decrease when vegetation provided concealment at these heights. If the current location of the bobwhite was unknown to the predator, I would expect cryptic behavior to be favored over behaviors that reveal its location (i.e., flushing). This is exacerbated by the fact that bobwhites are known to exhaust flushing capabilities after approximately 3 times in response to predators (Kassinis & Guthery, 1996). Bobwhites have been shown to select for areas of dense, tall vegetation after initiating flight escape (Perkins et al., 2014) showing variation in selection depending on threat type (i.e., aerial vs. terrestrial). This indicates bobwhites are capable of threat type detection and threat-sensitive predator avoidance responses (Helfman, 1989). Evidence for threat-sensitive behavior has been shown in other taxa such as fish (Brown & Dreier, 2002; Wishingrad et al., 2014), passerines (Freeberg et al., 2016; Turney & Godin, 2014) and ungulates (Creel et al., 2005; Kuijper, Bubnicki, Churski, Mols, & van Hooft, 2015).

I did not find any support to suggest that bobwhites were influenced by food availability while making decisions relating to escape behavior (Table 3.1 & 3.3). A potential explanation is that I could not discern active foraging behavior prior to encounter with hunters or that bobwhites located close to supplemental feed (majority of observations) are already satiated.

Food availability may take on different value to the animal dependent on the current behavioral state (Nathan et al., 2008; Stears & Shrader, 2015; Whittingham et al., 2006). With current technological advances in movement behavior research (Nathan et al., 2008), this may be a key avenue to study influences on perception of risk in future studies. Another potential explanation for this observed pattern is the length of the exposure period to hunters may not have been long enough to elicit a response in this context. Brief high-risk periods of predation should elicit intense anti-predator responses (Lima & Bednekoff, 1999). Food availability under these conditions may not matter for risk assessment because feeding can be immediately resumed once the threat has passed, but may matter in the context of longer exposure periods (D.McGrath, *in preparation*).

MANAGEMENT IMPLICATIONS

A decrease in RD by bobwhites can improve covey-detection rates (Radomski and Guthery 2000, Guthery 2002) because it allows hunters to approach coveys closer, and presumably are more easily observed or shot into. My results indicated that lower RDs (0.55 m) resulting from pointing by a scenting dog (Table 3.4), yielded higher detection and hunter-covey encounter rates. Predator (pointing dog) speed, also influences the total area covered during a hunting event—which in turn increases the probability of covey detection (Mecozzi & Guthery, 2007; Radomski & Guthery, 2000). An optimal combination of dog speed and pointing distance may improve rates of covey detection. Therefore, well-trained and appropriately conditioned dogs can help to locate and point coveys more quickly, at the appropriate distance for holding behavior (i.e., methodic trailing may increase response time and distance, thereby reducing covey detection rate), and maintain speed of hunting that maximizes covey detection rates.

Additional research on using multiple dog braces is warranted to better understand how spatial coverage using increased dog power influences covey detection.

Dense vegetation at approximately 0.60–1.30 m increased rates of holding behavior by bobwhite coveys in my study. This suggests that certain cover types and density are important for bobwhite concealment and predator avoidance strategies. Thus, intentional habitat management could improve covey-detection rates and hunter satisfaction. Whereas I did not find a particular cover type to be important (i.e. shrub cover), I suggest a mixture of vegetation types to create the concealment cover fancied by bobwhite coveys. I also found that increased exposure to firearm disengagement was an impetus for wariness-related behavior among bobwhite coveys, thereby increasing response distance and times and reducing overall covey detection. Limiting the number of time an area is hunted (<4 times) throughout the season on individual coveys may improve overall hunter satisfaction through increased covey encounters; if this is not possible, due to property constraints, we suggest increasing the speed of hunting, altering hunter behavior (approach speed to point), and altering hunting effort through temporal and spatial adjustments (see Chapter 2) to increase hunter-covey encounters. Successful escape behavior by bobwhite coveys is influenced by a myriad of these contextual factors as discussed previously. Future research investigating whether the success or failure of certain escape behaviors at one or more encounters dictates behavioral response by coveys at subsequent encounters is warranted.

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Table 3.1. Model selection results using deviance information criterion (DIC) of all mixed-effects Bayesian multinomial logit regression models for influences of our *a priori* hypotheses on factors influencing Northern Bobwhite escape behavior.

Model Name	*a priori* Hypothesis	DIC	ΔDIC
Pointed	Predator approach speed	201.54	0.00
Visual Obstruction @ 2 ft	Vegetation Density	202.58	1.04
Visual Obstruction @ 3 ft	Vegetation Density	202.74	1.21
Visual Obstruction @ 4 ft	Vegetation Density	204.38	2.85
NULL	Null	204.55	3.02
Distance to Supplemental Food	Food availability	205.56	4.03
Visual Obstruction @ 5 ft	Vegetation Density	205.92	4.39
% Shrub Composition	Vegetation Density	206.02	4.48
Previously Shot	Prior experience	206.14	4.60
% Grass Composition	Vegetation Density	206.44	4.90
Visual Obstruction @ 1 ft	Vegetation Density	206.50	4.96
Previously Encountered	Prior experience	206.85	5.31
% Open Ground	Vegetation Density	207.26	5.72
% Forb Composition	Vegetation Density	207.31	5.77
Previously Shot * Encountered	Prior experience	208.25	6.72
Previously Shot & Encountered	Prior experience	208.30	6.76

Table 3.2. Summary of top mixed-effects Bayesian multinomial logit regression models for influences of our *a priori* hypotheses on Northern Bobwhite escape behavior. All coefficients of behavioral effects need to be interpreted in accordance to our reference level, which is holding behavior. Model results shown all ranked above the null model of behavior. The Lower and Upper HPD's are the highest posterior density or 85% credibility intervals of the posterior distribution, while the Btail is the proportion of overlap that the posterior distribution shares with zero. Both metrics are used to assess biological meaning of the estimates.

Model	Variables	Mean	SD	Naïve SE	Mode	Btail	Lower HPD	Upper HPD
Pointed	Flush	-0.158	0.466	0.005	-0.234	0.358	-1.056	0.771
	Run	-1.276	0.552	0.006	-1.266	0.010	-2.349	-0.193
	Days into season	0.038	0.293	0.003	0.073	0.560	-0.546	0.604
	Flush:Pointed	-1.205	0.672	0.007	-0.988	0.033	-2.550	0.094
	Run:Pointed	0.427	0.683	0.007	0.383	0.733	-0.955	1.733
Visual Obstruction @ 0.6 m	Flush	-0.782	0.357	0.004	-0.811	0.013	-1.278	-0.262
	Run	-0.995	0.365	0.004	-0.956	0.004	-1.506	-0.470
	Days into season	-0.031	0.292	0.003	-0.051	0.460	-0.441	0.387
	Flush:VOR	-0.751	0.369	0.004	-0.775	0.015	-1.279	-0.222
	Run:VOR	-0.065	0.344	0.003	-0.107	0.428	-0.563	0.419
Visual Obstruction @ 1 m	Flush	-0.768	0.353	0.004	-0.773	0.014	-1.276	-0.271
	Run	-0.988	0.361	0.004	-1.051	0.004	-1.515	-0.488
	Days into season	0.012	0.281	0.003	-0.002	0.523	-0.394	0.404
	Flush:VOR	-0.760	0.364	0.004	-0.713	0.013	-1.258	-0.220
	Run:VOR	-0.207	0.339	0.003	-0.251	0.272	-0.671	0.299
Visual Obstruction @ 1.2 m	Flush	-0.775	0.370	0.004	-0.882	0.017	-1.269	-0.215
	Run	-0.979	0.381	0.004	-0.970	0.006	-1.536	-0.456
	Days into season	0.020	0.286	0.003	0.101	0.536	-0.372	0.447
	Flush:VOR	-0.829	0.458	0.005	-0.757	0.020	-1.429	-0.163
	Run:VOR	-0.205	0.369	0.004	-0.145	0.299	-0.713	0.322

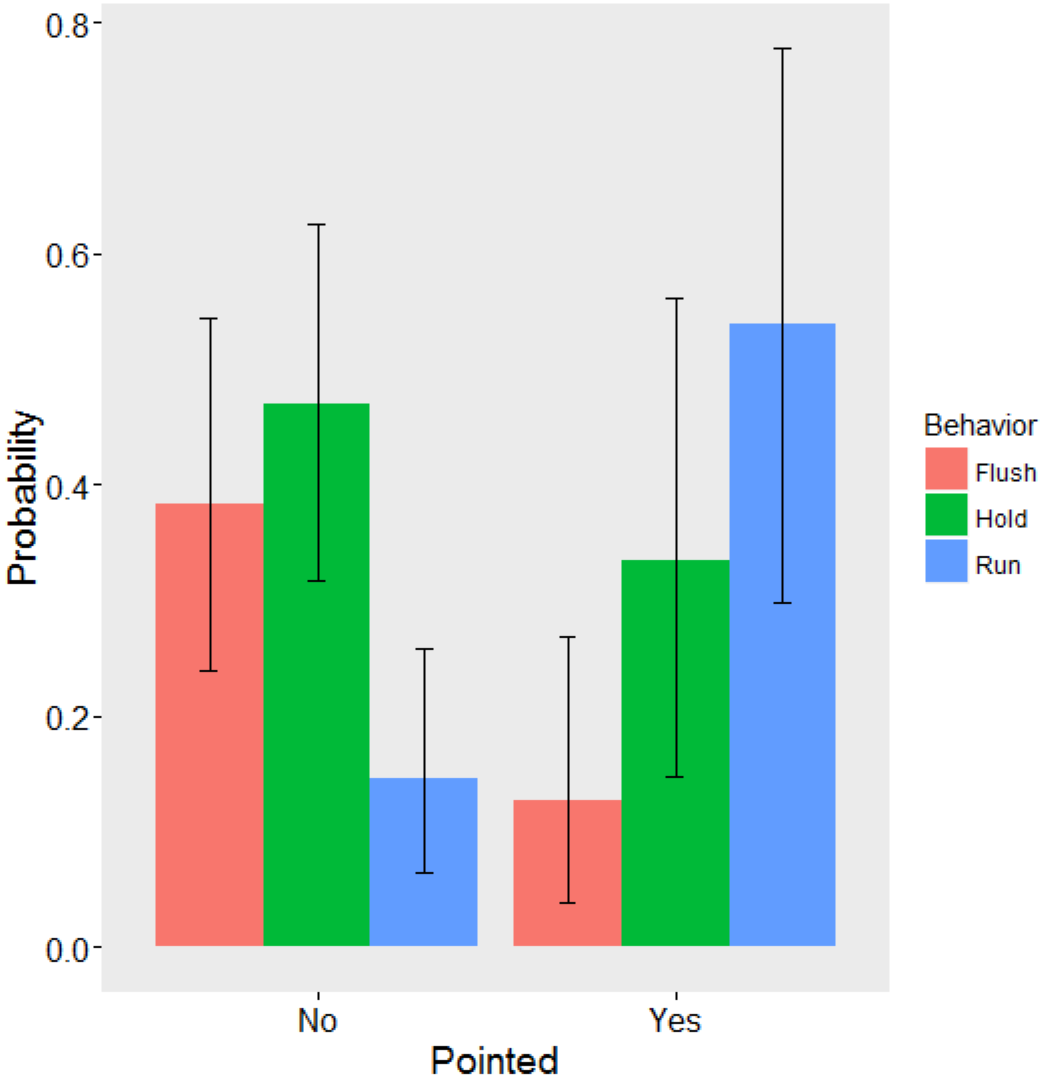

Figure 3.1. Effect of pointing dog status on probability of evasive tactic of Northern Bobwhites during encounters with hunters (*n*= 97). Error bars represent the 85% credibility interval around posterior means. Data was collected from the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. When pointing dogs successfully held point, the probability of bobwhites flushing decreases.

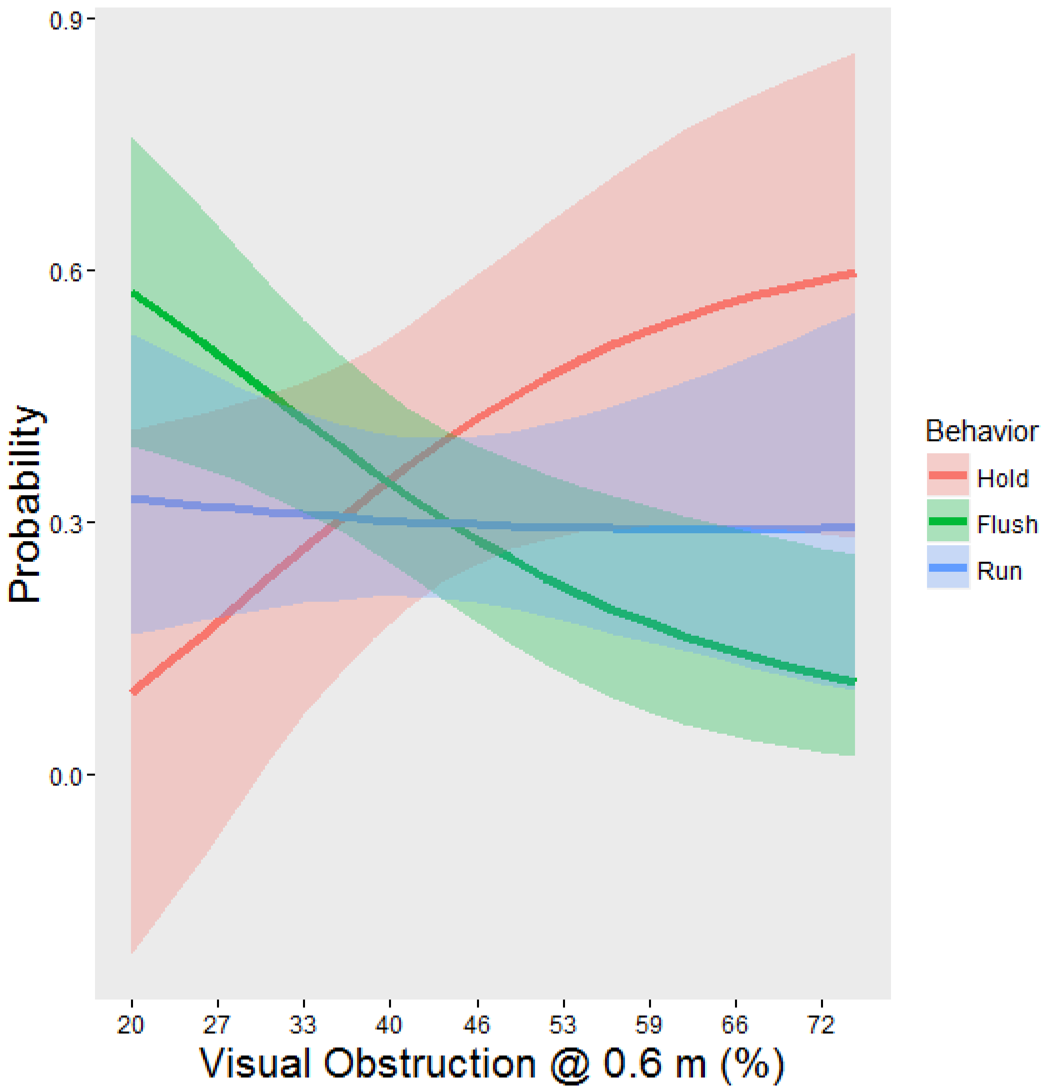

Figure 3.2. Effect of visual obstruction at 0.6 m on probability of evasive tactic of Northern Bobwhites during encounters with hunters (*n*= 97). Colored ribbons represent the 85% credibility interval around posterior means. Data was collected from the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. As visual obstruction increases at 0.6 m probability of holding behavior increases.

Table 3.3. Model selection results using ΔAIC_c and model fit results using marginal and conditional R^2 of linear mixed-effect models on the influence of our *a priori* hypotheses on response distance of Northern Bobwhites escape behavioral tactics.

Model Name	*a priori* Hypothesis	K	AICc	ΔAICc	w_i	Res LL	R^2M	R^2C
Visual Obstruction @ 0.3 m	Vegetation Density	7	399.209	0.000	0.516	-191.976	0.167	0.190
Pointed	Predator approach speed	7	402.703	3.493	0.090	-193.722	0.138	0.164
Previously Shot	Prior experience	7	402.879	3.670	0.082	-193.811	0.146	0.205
Visual Obstruction @ 0.6 m	Vegetation Density	7	403.011	3.802	0.077	-193.876	0.134	0.155
NULL	Null	6	403.968	4.759	0.048	-195.518	0.105	0.114
% Forb Composition	Vegetation Density	7	404.807	5.597	0.030	-194.774	0.117	0.117
Previously Encountered	Prior experience	7	405.197	5.987	0.026	-194.969	0.117	0.141
Previously Shot & Encountered	Prior experience	8	405.243	6.033	0.025	-193.803	0.145	0.209
Visual Obstruction @ 1.5 m	Vegetation Density	7	405.264	6.055	0.025	-195.003	0.113	0.120
Distance to Feed	Food availability	7	405.636	6.426	0.021	-195.189	0.110	0.111
Visual Obstruction @ 1 m	Vegetation Density	7	405.700	6.490	0.020	-195.221	0.110	0.123
% Open Ground	Vegetation Density	7	405.988	6.778	0.017	-195.365	0.107	0.123
Visual Obstruction @ 1.2 m	Vegetation Density	7	406.253	7.043	0.015	-195.497	0.105	0.115
% Grass Composition	Vegetation Density	7	406.286	7.076	0.015	-195.514	0.104	0.113
% Shrub Composition	Vegetation Density	7	406.289	7.080	0.015	-195.516	0.104	0.114
Previously Shot * Encountered	Prior experience	9	407.621	8.412	0.008	-193.776	0.145	0.212

Table 3.4. Summary of effect sizes from top linear mixed-effect models (ranking above null model), for influences of our *a priori* hypotheses on response distance of Northern Bobwhite escape behavior. All coefficients shown in bold have 85% CL that do not overlap zero and therefore can be interpreted as biologically significant.

Model Name	Model Variables	B	SE	LCL – (85%)	UCL – (85%)
Visual Obstruction @ 0.3 m	Intercept	1.857	0.254	1.491	2.223
	Days into season	-0.139	0.205	-0.434	0.155
	Flush	-0.265	0.424	-0.876	0.346
	Run	**1.036**	**0.461**	**0.372**	**1.699**
	VOR	**0.555**	**0.204**	**0.261**	**0.848**
Pointed	Intercept	2.321	0.332	1.843	2.799
	Days into season	-0.440	0.186	-0.708	-0.172
	Flush	-0.520	0.437	-1.150	0.109
	Run	**0.965**	**0.467**	**0.292**	**1.638**
	Pointed	**-0.730**	**0.377**	**-1.273**	**-0.186**
Previously Shot	Intercept	1.666	0.291	1.247	2.086
	Days into season	**-0.544**	**0.201**	**-0.833**	**-0.254**
	Flush	-0.453	0.431	-1.074	0.168
	Run	**0.867**	**0.467**	**0.195**	**1.539**
	Shot	**0.550**	**0.274**	**0.157**	**0.944**
Visual Obstruction @ 0.6 m	Intercept	1.870	0.259	1.497	2.243
	Days into season	-0.301	0.192	-0.578	-0.025
	Flush	-0.216	0.439	-0.849	0.416
	Run	**0.906**	**0.467**	**0.234**	**1.578**
	VOR	**0.356**	**0.194**	**0.077**	**0.636**

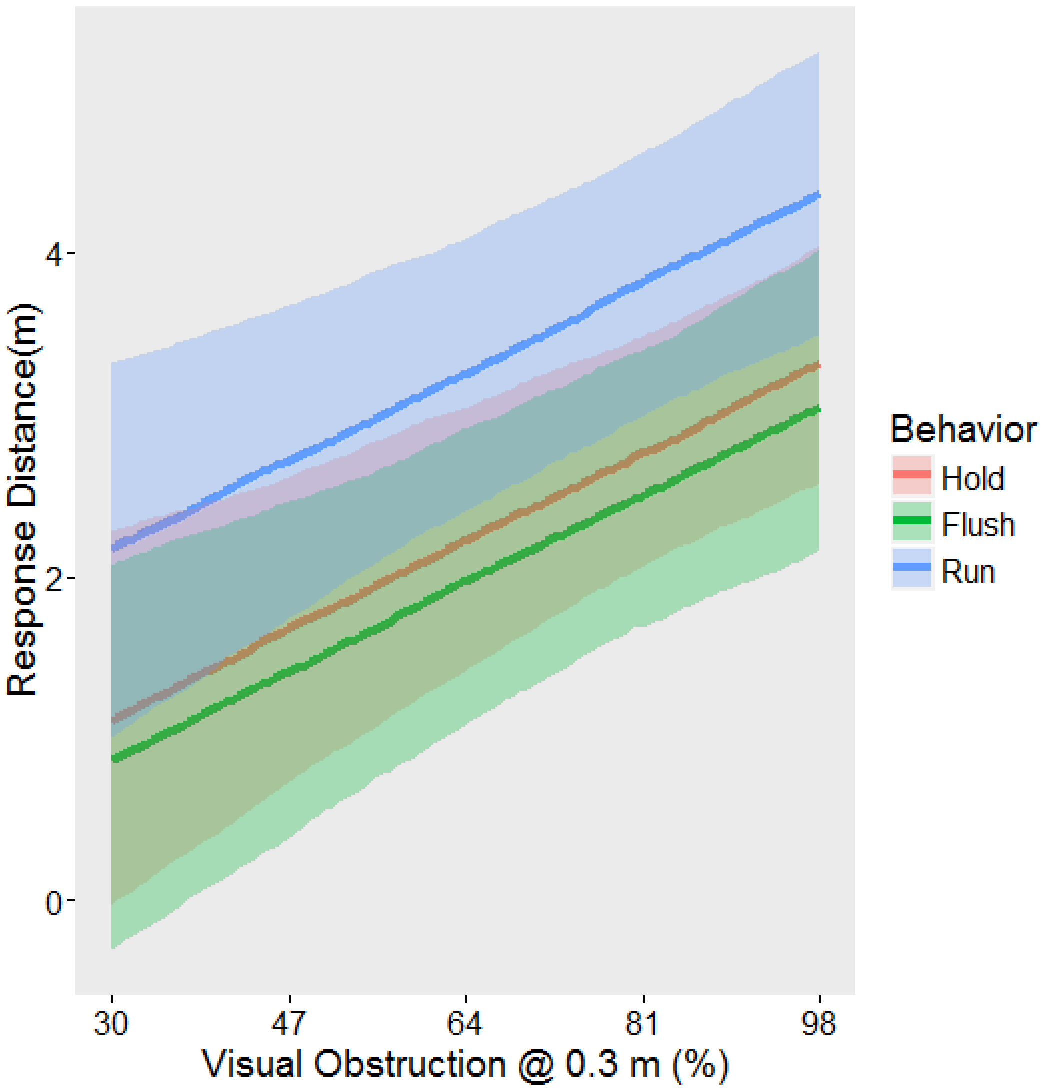

Figure 3.3. Effect of visual obstruction at 0.3 m on response distance of evasive tactics of Northern Bobwhites during encounters with hunters (*n*= 97). Error ribbons represent the 85% credibility interval around posterior means. Data was collected from the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. As visual obstruction increases at 0.3 m probability response distance for all evasive tactics increases.

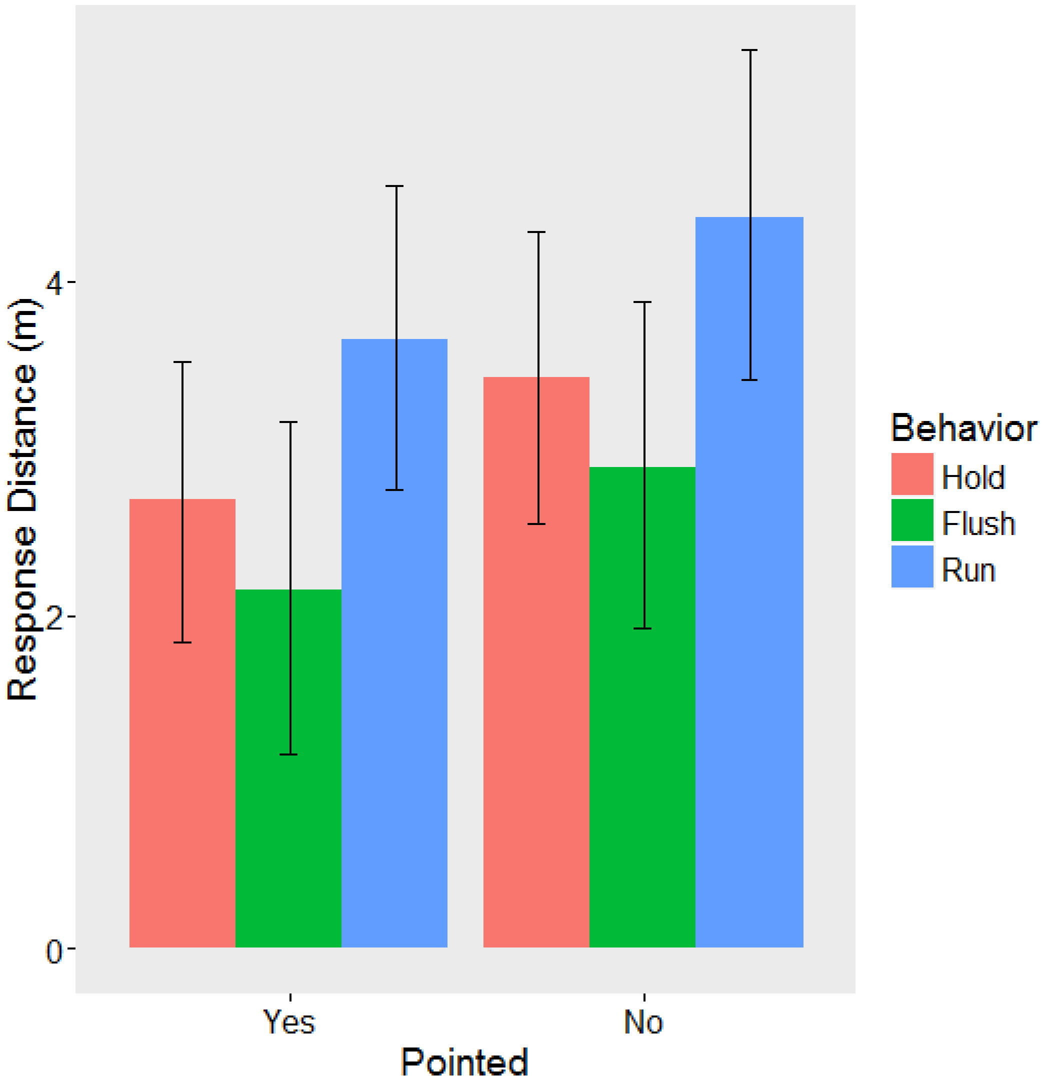

Figure 3.4. Effect of pointing dog status on response distance of evasive tactics of Northern Bobwhites during encounters with hunters (*n*= 97). Error bars represent the 85% credibility interval around posterior means. Data was collected from the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. Response distance decreased when pointing dogs successfully held point.

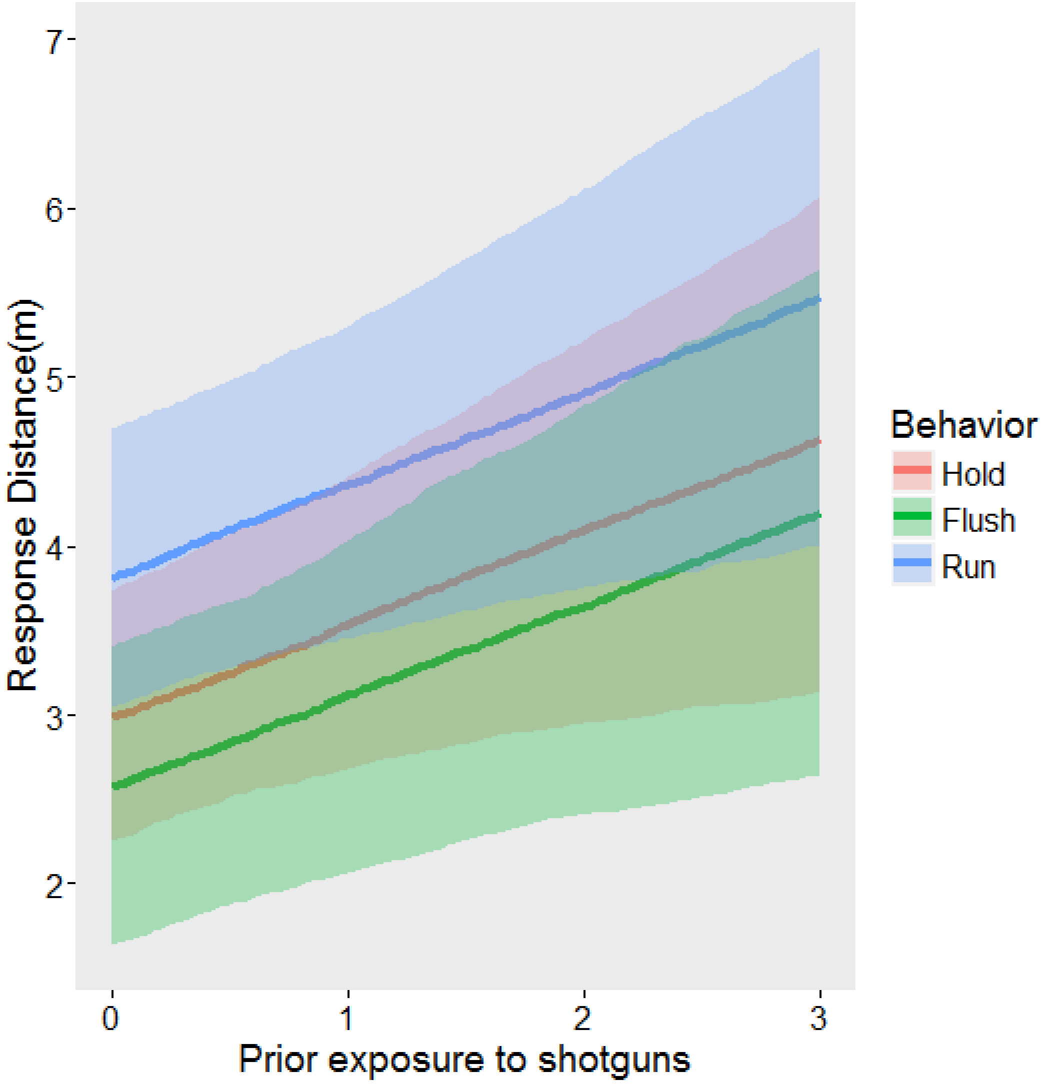

Figure 3.5. Effect of prior exposure to shotguns on response distance of evasive tactics of Northern Bobwhites during encounters with hunters (*n*= 97). Error ribbons represent the 85% credibility interval around posterior means. Data was collected from the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. Response distance increased when bobwhites had more exposure to shotguns.

CHAPTER 4

SYNTHESIS AND MANAGEMENT IMPLICATIONS

My research indicates that bobwhites have both direct and indirect behavioral responses to mitigate the effects of hunting pressure. I found that bobwhites altered their foraging strategies to mitigate future exposure to hunters (i.e., an indirect behavioral response). These included a decrease in foraging duration and area, and an increase in bout frequency in response to exposure to hunters. I found evidence for a temporal shift in foraging behavior away from periods of high hunting pressure, lending support to the risky times hypothesis. I found a lack of support for the risky spaces hypothesis such that they used areas of increased risk of hunters with increasing exposure levels—until bobwhites were encountered four times. However, on my study site, areas of increased risk (i.e., repetitive hunting) were also proximate to supplemental feed suggesting that bobwhites may have been increasing their feeding efficiency per unit time to make up for decreased foraging bouts.

I found evidence for the influence of several factors in terms of willingness to tolerate risk and choice of evasive tactic in direct response to a hunting encounter (i.e., a direct behavioral response). I found that predator approach speed (i.e., when a scenting dog was actively moving) positively influenced the probability of flushing (a more energetically costly escape behavior) compared to holding. I also found that vegetation density at 0.6, 1.0, and 1.2 m decreased the probability of flushing compared to holding. In terms of response distance, I found that bobwhites were less willing to tolerate risk under several conditions including when:

scenting dogs were actively moving, they had previous exposure to firearms and vegetation density was high at 0.3 and 0.6 m.

In both studies I found evidence for bobwhites having a greater behavioral response to the threat of hunters discharging firearms as compared to hunter encounters when firearms were not discharged. This result gives direct support to the threat-sensitive predator avoidance hypothesis as it suggests bobwhites are cognitively capable of assessing the magnitude of a given threat. I also found several situations where bobwhites responded to cumulative levels of hunting pressure further suggesting that bobwhites are capable of learning patterns in human hunting, have some form of memory capabilities and are able to behaviorally respond to such information.

Taken collectively my results have several implications for bobwhite managers. My results on bobwhite foraging strategies suggest that bobwhites were able to compensate for a decrease in foraging duration and area with an increased use of supplemental feed and more frequent foraging bouts. This would suggest that the presence of supplemental feed counteracted potential negative effects on fitness due to non-consumptive effects of hunting pressure. However, this implication would need further support from experimental research controlling levels of supplemental feed (i.e., presence vs. absence) to say the effect is truly compensatory. Secondly, the results from my foraging study suggested that bobwhites were able to learn the temporal pattern of hunters. This suggests that hunters should try to limit the repetitiveness or bias in their hunting regimes both spatially and temporally.

The results from my escape behavior study suggest several factors are important to bobwhites in terms of willingness to tolerate risk. My results showed the importance of scenting dogs in improving response distance of bobwhite escape behaviors for the benefit of hunters.

This suggests that dogs trained to point coveys at intermediate distances (i.e., 5 m as compared to 1 m) may improve the possibilities of a bobwhite-hunter encounter. Further the speed of the hunting party can improve the total area coverage during a given hunt—a component known to improve covey detections. My research suggests that by increasing hunt pace but maintaining a decent distance at detection would further improve covey detections.

My research showed dual effects of vegetation density on escape behavior and therefore threat perception. At 0.3 m, dense vegetation was shown to be obstructive (i.e., increase in RD) but at greater heights vegetation density was shown to be protective (i.e., decrease in probability of flushing compared to holding). I suggest that managers should create a matrix of concealment and openness at 0.3 m for bobwhites to feel protected and therefore be more likely to hold in response to hunters compared to flushing, also improving the probability of detections. I am not suggesting a lack of vegetation at 0.3 m but rather vegetation that does not prevent visual obstruction (i.e., no dense grasses for an extended area).

My research highlights the importance of understanding behavioral responses to predation pressure, a largely understudied aspect of bobwhite ecology. Several of my models incorporated a random effect of covey ID. In my research design this was to control for variation due to bobwhites the influence of group dynamics on behavior. Future research should focus on determining the specific group dynamics (i.e., size, age structure or animal personalities) that influence behavioral processes such as foraging or escape behavior. Foraging strategies may vary seasonally depending on what other processes are important during that time period. My study was conducted during winter, when overwinter survival is the primary driver of behavior. However, foraging patterns may be very different during the spring/ summer season when bobwhites must allocate time between foraging and breeding activities. This technique could also be used to compare foraging strategies in other regions of bobwhite habitat where food resources may be spatially or temporally different. The use of fine scale movement data such as what was collected here may allow for further insight into how bobwhites handle competing behaviors.

APPENDIX A

VISUAL REPRESENTATION OF FORAGING VARIABLES AND HUNTING METRICS

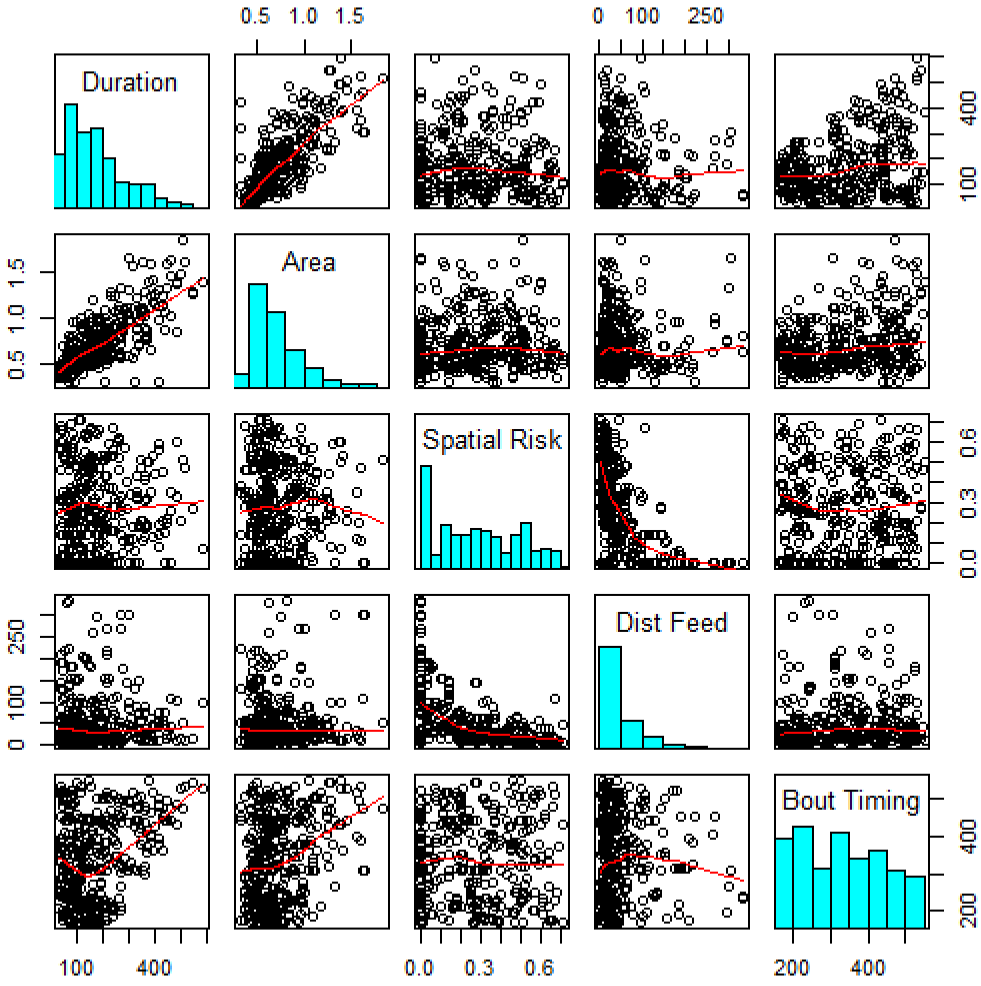

Figure 1. Distributions and correlations of all foraging variables at the bout level (*n*= 744) of Northern Bobwhites during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina.

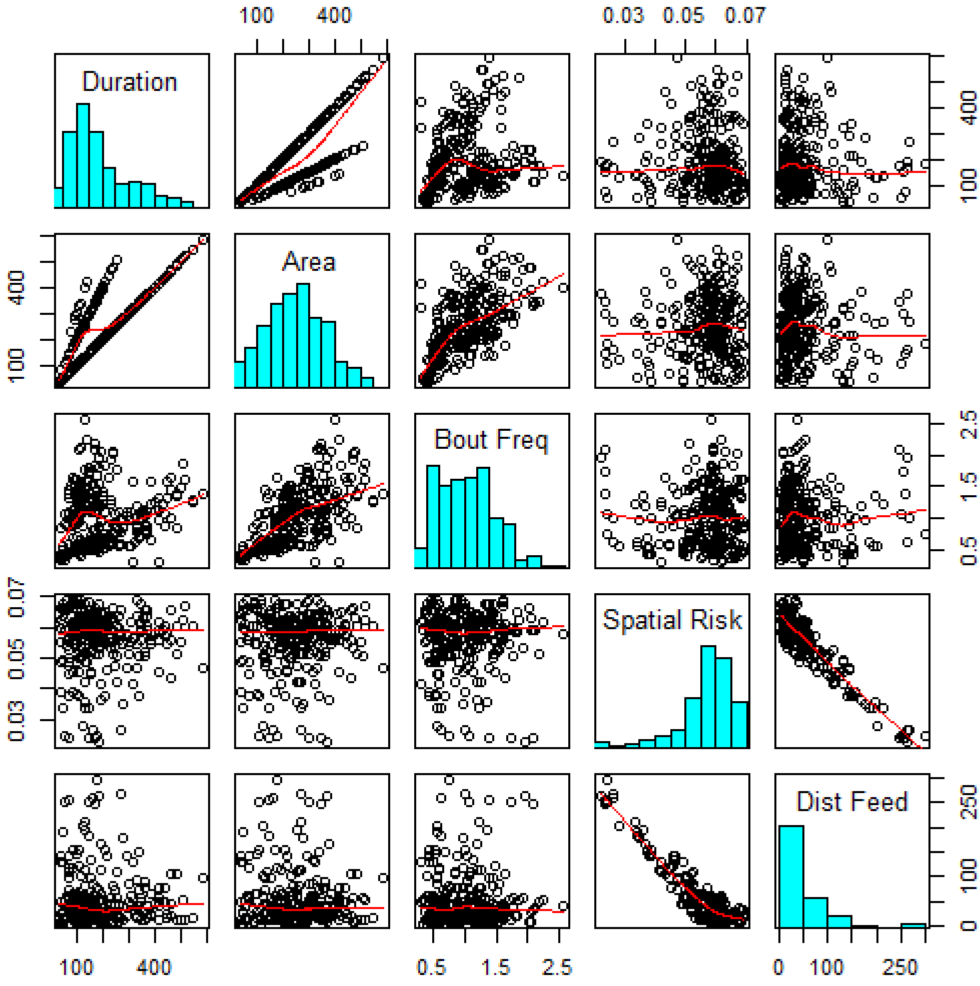

Figure 2. Distributions and correlations of all foraging variables at the daily level (*n* = 514) of Northern Bobwhites during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina.

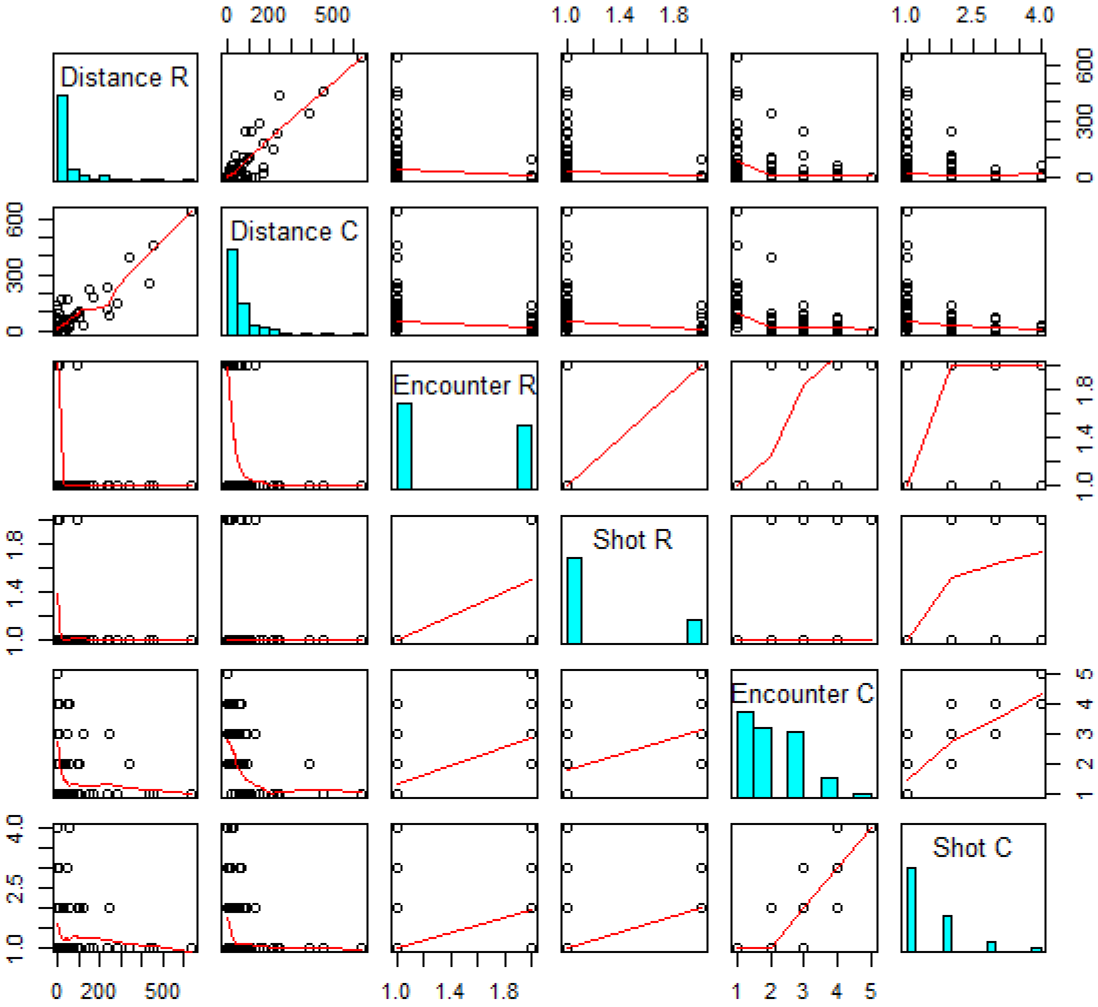

Figure 3. Distributions and correlations of all hunting metrics of Northern Bobwhites during the winter of 2014–2015 on a private plantation in Georgetown County, South Carolina. Recent encounter metrics are represented with an R while cumulative metrics are represented with a C. Previous number of encounters and exposure to shotguns are factors.

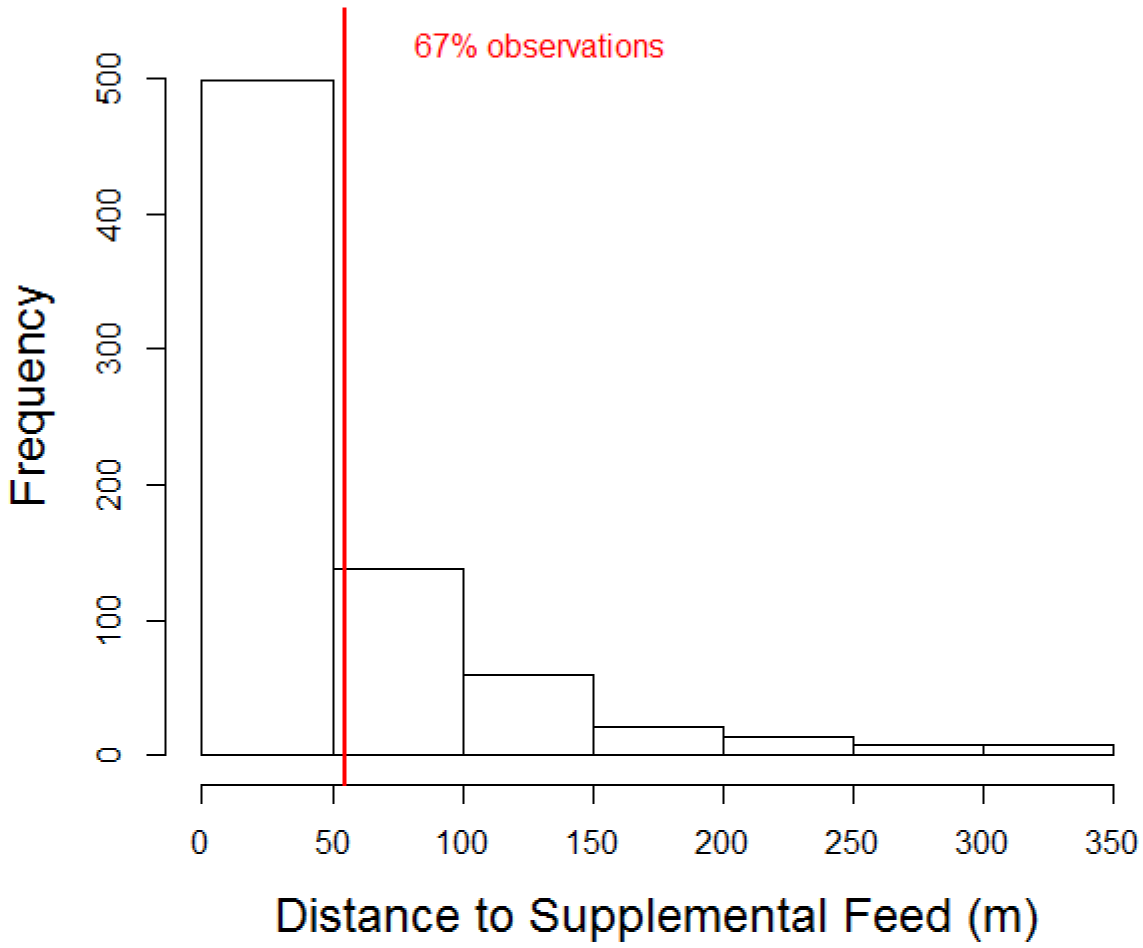

Figure 4. Distance to supplemental feed of all movement paths identified as foraging bouts (*n*= 744) of Northern Bobwhites during the winter of 2014–2015 on a private property in Georgetown county, South Carolina. The red line indicates 67% of all foraging bouts occurred within 50 m of the feedline, showing a bias in foraging behavior for supplemental feed usage.

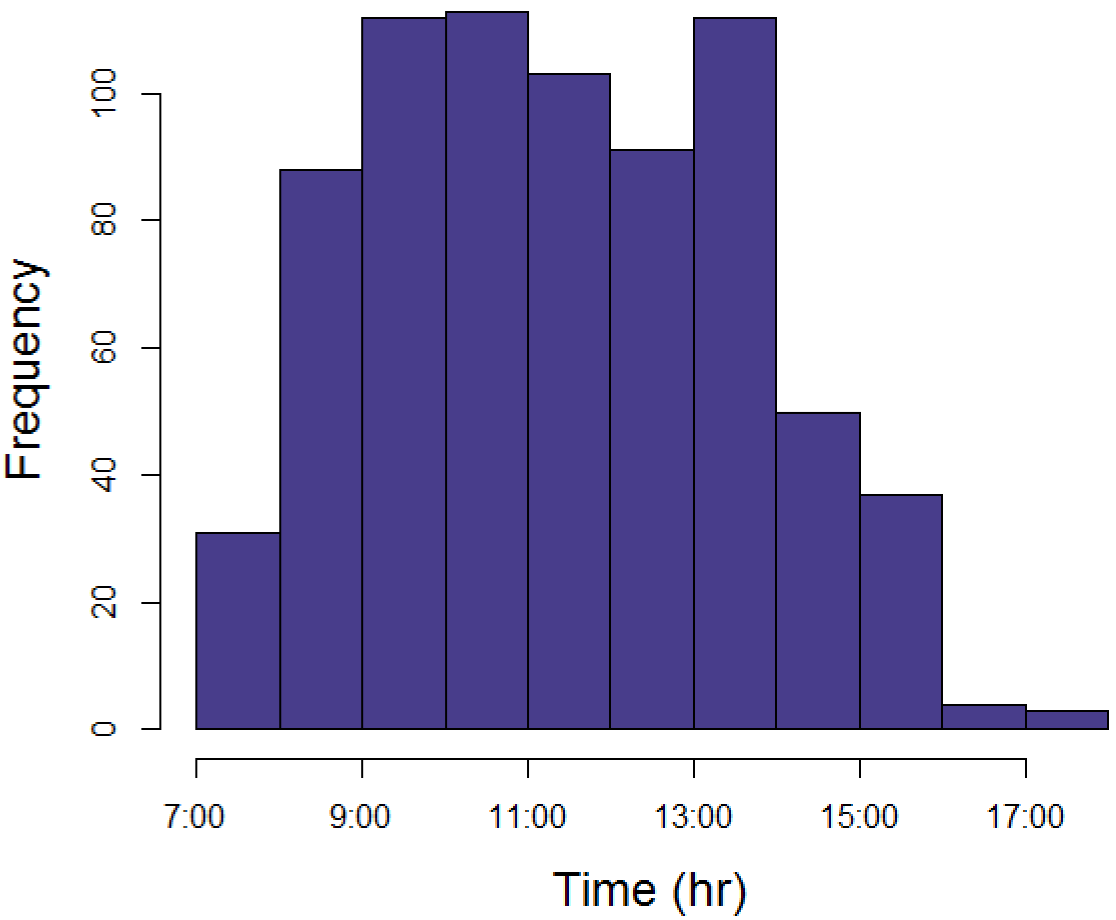

Figure 5. Start time for all movement paths identified as foraging bouts (*n* = 744) of Northern Bobwhites during the winter of 2014–2015 on a private property in Georgetown county, South Carolina. Average start time for foraging was 11:24 (SD=2.2 hrs).

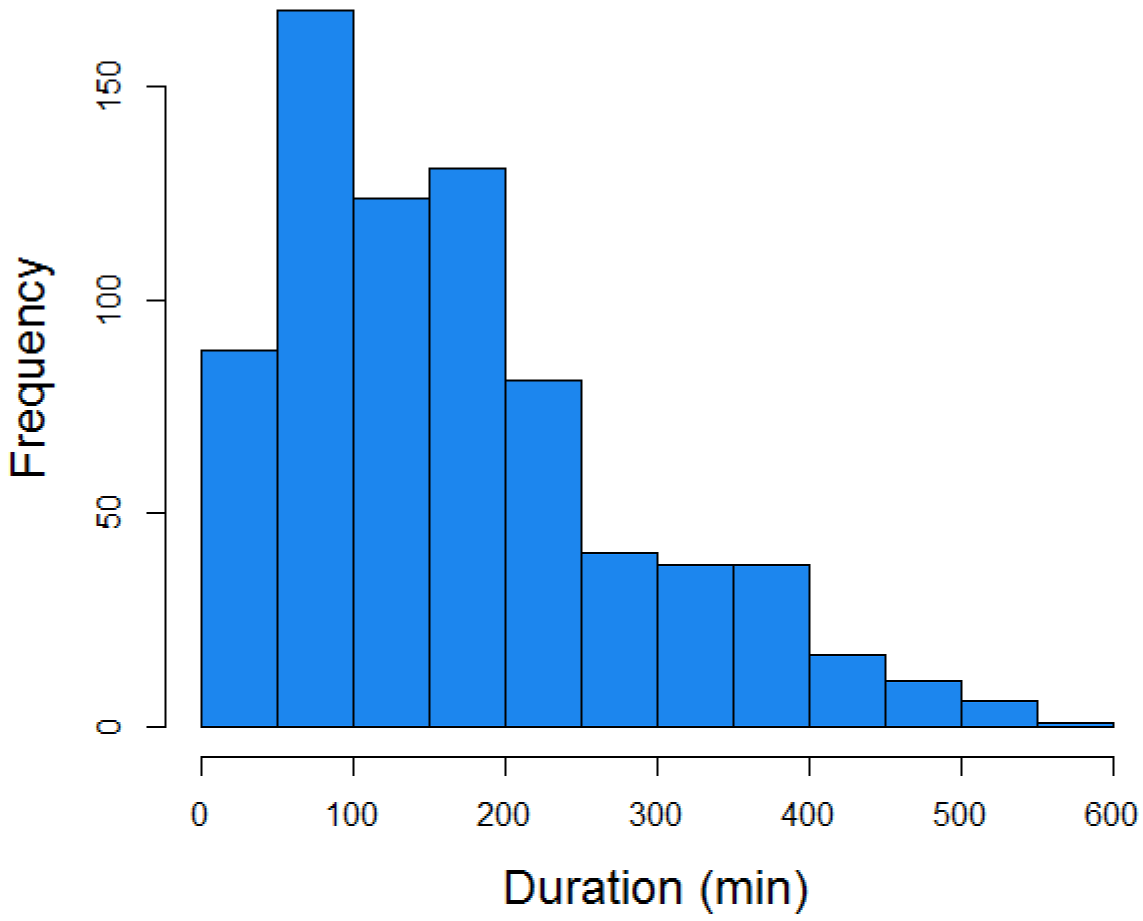

Figure 6. Duration for all movement paths identified as foraging bouts (*n* = 744) of Northern Bobwhites during the winter of 2014–2015 on a private property in Georgetown county, South Carolina. Average duration for foraging was 169 mins (SD = 249).

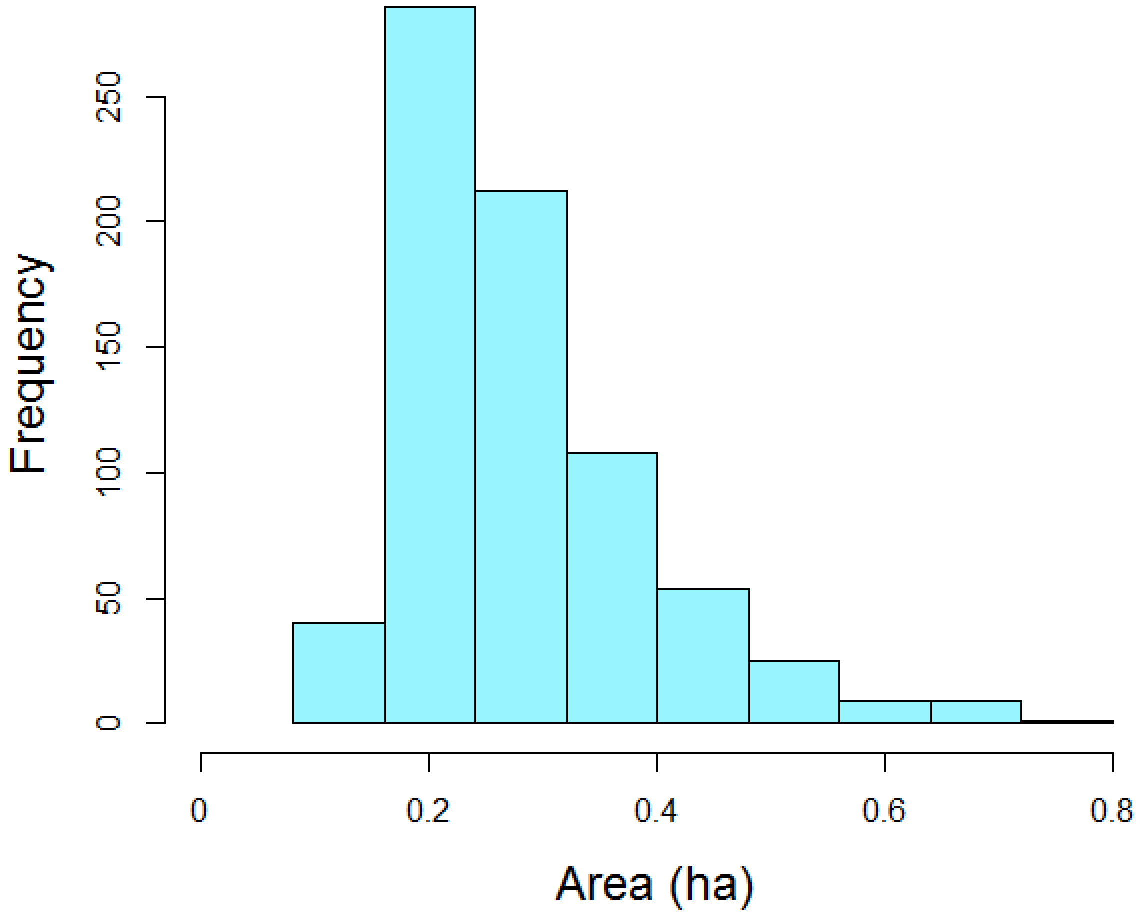

Figure 7. Area for all movement paths identified as foraging bouts (*n* = 744) of Northern Bobwhites during the winter of 2014–2015 on a private property in Georgetown county, South Carolina. Average start time for foraging was 0.42 ha (SD = 0.17).

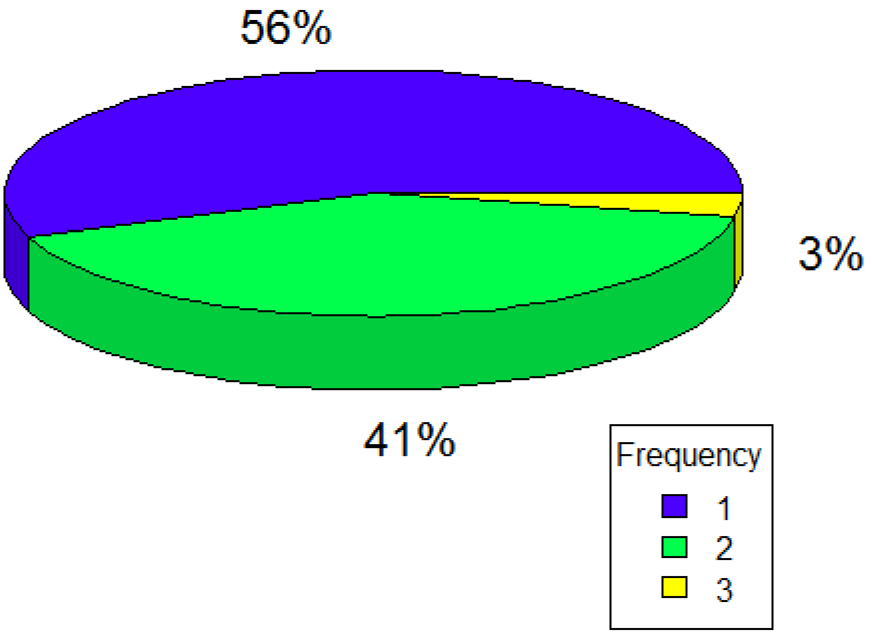

Figure 8. Frequency of foraging bouts per day (*n* = 514) of Northern Bobwhites during the winter of 2014–2015 on a private property in Georgetown county, South Carolina. Frequencies of bouts ranged from 1–3 bouts per day and occurrence rates are represented next to each slice on the graph.

APPENDIX B

VISUAL REPRESENTATION OF BEHAVIORAL METRICS AND HUNTER OBSERVATIONS

Table 1. Correlation matrix of relatedness using Pearson's correlation (*r*) values between all vegetation metrics taken at 97 encounter locations during the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina.

	Grass	Forb	Rubus	Shrub	Ground	VOR @ 0.3 m	VOR @ 0.6 m	VOR @ 1.0 m	VOR @ 1.2 m	VOR @ 1.5 m
Grass	1.000	-0.289	-0.304	-0.308	-0.259	0.064	-0.165	-0.171	-0.149	-0.154
Forb	-0.289	1.000	0.350	-0.227	-0.035	0.104	0.130	0.115	0.103	-0.056
Rubus	-0.304	0.350	1.000	-0.180	-0.206	0.139	0.120	0.087	0.077	0.009
Shrub	-0.308	-0.227	-0.180	1.000	0.089	0.280	0.451	0.371	0.173	0.163
Ground	-0.259	-0.035	-0.206	0.089	1.000	-0.327	-0.052	0.066	0.075	0.021
VOR @ 0.3 m	0.064	0.104	0.139	0.280	-0.327	1.000	0.659	0.378	0.100	-0.012
VOR @ 0.6 m	-0.165	0.130	0.120	0.451	-0.052	0.659	1.000	0.820	0.446	0.204
VOR @ 1.0 m	-0.171	0.115	0.087	0.371	0.066	0.378	0.820	1.000	0.737	0.418
VOR @ 1.2 m	-0.149	0.103	0.077	0.173	0.075	0.100	0.446	0.737	1.000	0.732
VOR @ 1.5 m	-0.154	-0.056	0.009	0.163	0.021	-0.012	0.204	0.418	0.732	1.000

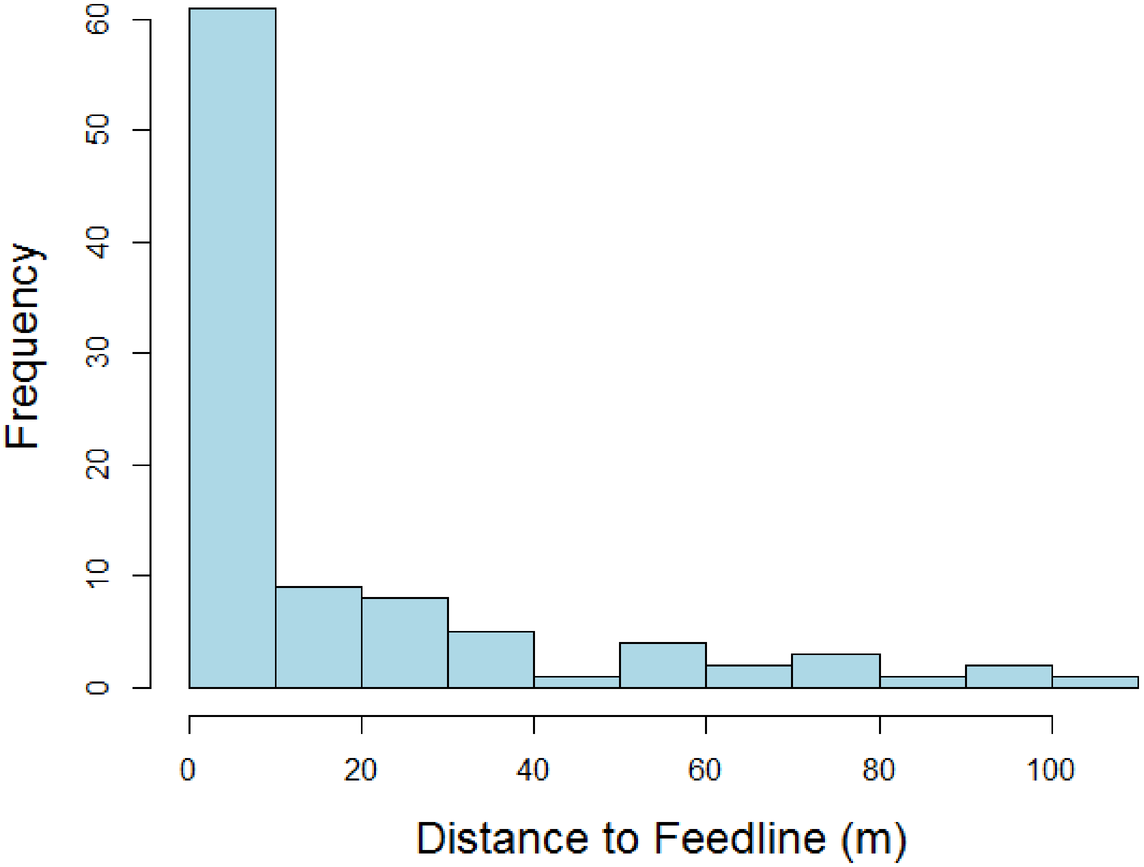

Figure 1. Distribution of encounter locations (*n*= 97) in regards to distance to feedline during the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. Observations are biased to proximate distance to supplemental feed due to hunting bias in favoring that area.

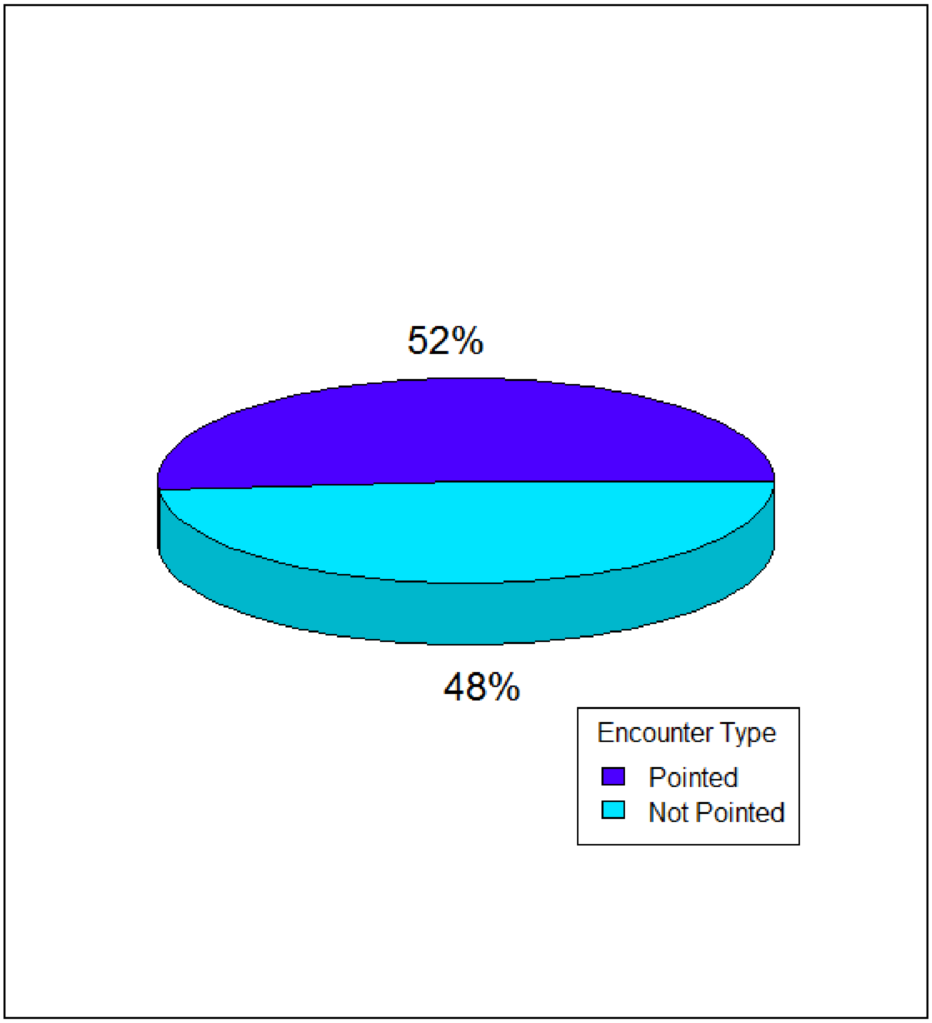

Figure 2. Frequencies of pointing dog status during all encounter (*n* = 97) of Northern Bobwhites during the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina.

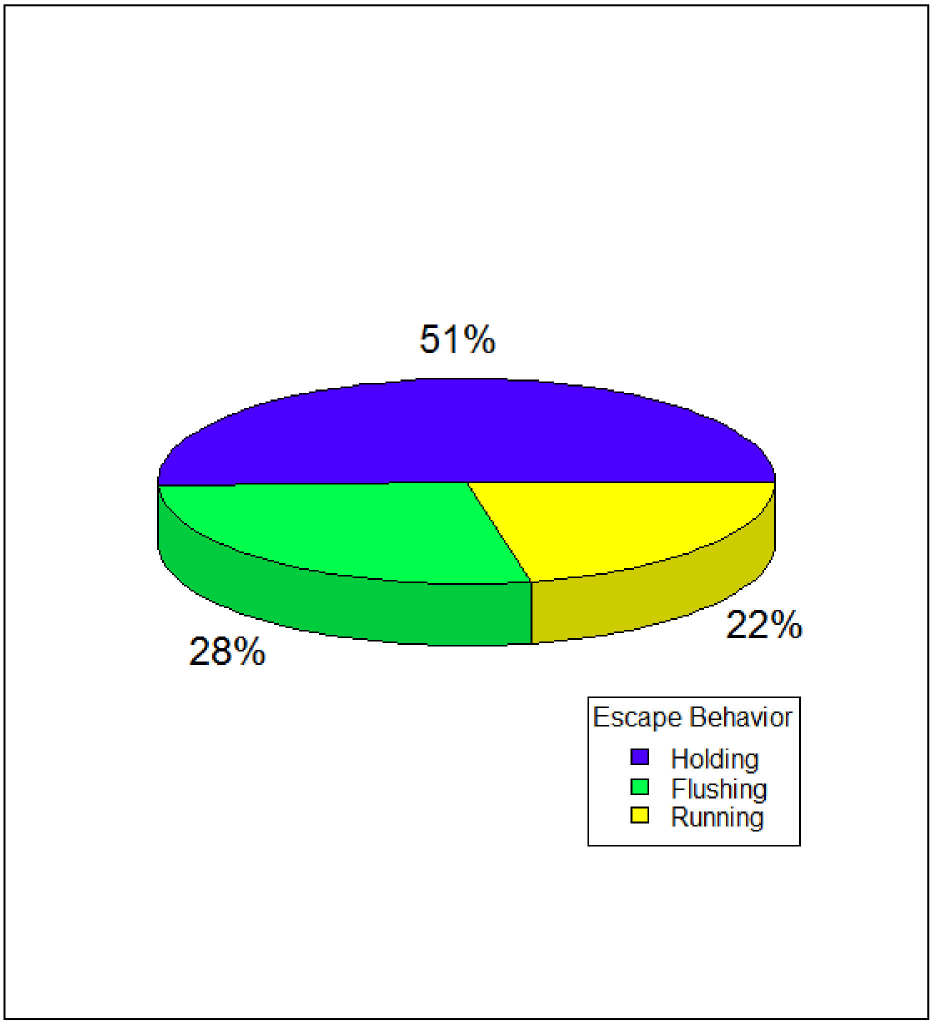

Figure 2. Frequencies of Northern Bobwhite evasive tactic during all encounter (*n* = 97) of Northern Bobwhites during the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina.

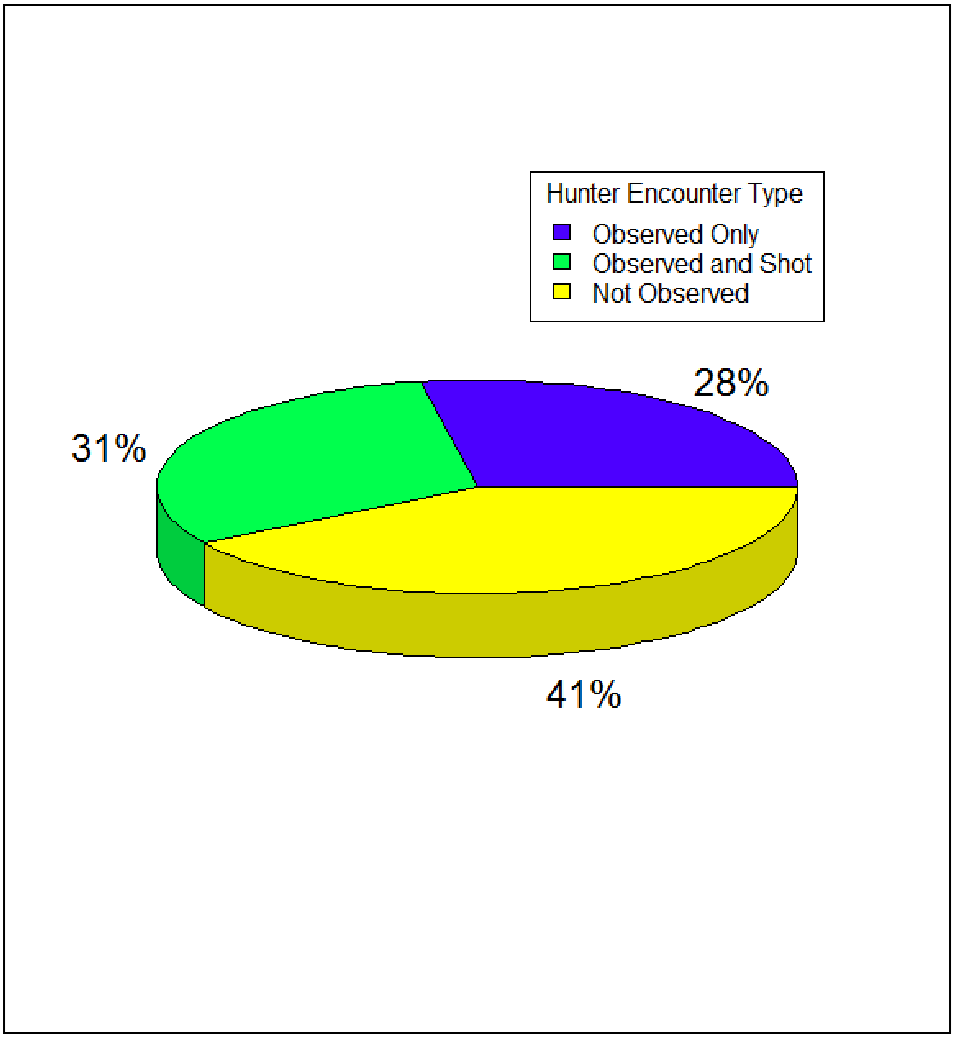

Figure 3. Frequencies of hunter encounter type during all encounter (*n* = 97) of Northern Bobwhites during the winters of 2013–2014 and 2014–2015 on a private property in Georgetown county, South Carolina. Encounters where bobwhites were pointed by a pointing dog but failed to be visually observed by the hunting party are labeled as “not observed”.