CASCADING EFFECTS OF HUNTING DISTURBANCE ON NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*) BEHAVIOR, PHYSIOLOGY, AND SURVIVAL

by

EMILY NICOLE PROSSER

(Under the Direction of James A. Martin)

ABSTRACT

Northern Bobwhites (*Colinus virginianus*) are an important gamebird across the United States and have been in decline for several decades. As a commonly hunted prey species, bobwhite provide an ideal study species to investigate the use of proactive and reactive anti-predator behaviors in response to hunting pressure. We designed an experiment to understand how late season hunting affects bobwhite demographics using fecal glucocorticoid (*f*GCM) concentrations, foraging and movement behaviors, survival, and breeding season metrics. Our results show that bobwhite responded to increased interactions with a shotgun through proactive responses. After one encounter with a discharged shotgun, bobwhite foraged further from supplemental feed where the risk of encountering a hunting party was the greatest. Bobwhite responded to increased hunting pressure, particularly late season hunting pressure, via reactive responses through increased *f*GCM concentrations, resulting in decreased fecundity. These results can help inform hunting season regulations and management decisions aiding in bobwhite recovery.

INDEX WORDS: *Colinus virginianus*, bobwhite, antipredator behavior, glucocorticoid, non-consumptive effects, hunting pressure, fecundity, ecology of fear, stress, fecal corticosterone

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DEDICATION

I would like to dedicate this thesis to my parents: Barbara and Rodney. They fostered my love for the natural world and taught me the value of independence, perseverance, and dedication. Their unconditional support throughout my graduate career and many jobs across the country has helped me get to where I am today. Their encouragement has helped me to achieve this accomplishment and I cannot thank them enough.

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CHAPTER 1

GENERAL INTRODUCTION

The Northern Bobwhite (*Colinus virginianus*; hereafter, bobwhite) is an important gamebird both economically and culturally in many rural communities across the southeastern United States (Guthery et al. 2004). However, populations have steadily declined since the early 20th century due to habitat loss and fragmentation (Brennan 1991). Many studies have focused on habitat management on private and public lands, but few have investigated the impacts of anthropogenic stressors on bobwhite physiology and demography. As a prey species, bobwhite live within an anthropogenic landscape of fear and by understanding the consequences of anti-predator behaviors used to mitigate those fears, managers and biologists can make informed decisions on how regulations may impact body condition and the survival of the population (Little et al. 2014, Creel 2018).

When faced with the risk of predation, prey engage in anti-predator decision making and respond with proactive or reactive responses (Lima 1998, Creel 2018). When a threat is predictable, prey may use past experiences and learned behaviors to make decisions that proactively mitigate the risk (Atuo and O'Connell 2017, Creel 2018). Under the predator-sensitive food hypothesis, prey weigh the benefits of foraging with the possible risk for predation and as a result, they may spatially or temporally alter foraging patterns to reduce their chances of interacting with a predator (Sinclair and Arcese 1995, Heithaus et al. 2009, Matassa and Trussel 2011, McGrath et al. 2018).

Heithaus et al. (2009) found that pied cormorants (*Phalacrocorax* varius) shifted foraging away from prey-rich habitats with higher tiger shark (*Galeocerdo* cuvier) densities to habitats where prey were less abundant, but tiger sharks posed less of a threat (Heithaus et al. 2009). This type of proactive, anti-predator decision making can be seen across taxa in a variety of species including bobwhite, elk (*Cervus canadensis*), and vervet monkeys (*Cercopithecus aethiops*) (Willems and Hill 2009, McGrath et al. 2018, Spitz et al. 2019).

If a threat is unpredictable or uncontrollable, prey may respond with reactive behaviors. Reactive behaviors can be observed in types of behavior modification including fleeing an attack or in the form of physiological changes (Creel 2018). Following the predator-induced stress hypothesis, when prey encounter threats such as predators or human hunters, the hypothalamic-pituitary-adrenal axis (HPA axis) is activated and glucocorticoid concentrations in the blood are elevated (Dantzer et al. 2014). Acute, temporary spikes in glucocorticoids allow the body to focus resources on areas needed to enable the ‘fight-or-flight’ response (Sapolsky et al. 2000). Once the threat is over, the individual is able to reestablish homeostasis preventing negative consequences on body condition (Sapolsky et al. 2000). If these responses occur too often, individuals are not able to return to homeostasis and they enter a constant state of fear resulting in chronic stress. Chronic stress can impede the natural functions of the body and have a negative impact on body condition ultimately decreasing fecundity and survival (Sapolsky et al. 2000, Sheriff et al. 2009). The physiological impacts of corticosterone and its effects on demography can be a complex system and it is important to understand how proactive and reactive responses influence behavior modification and body condition (Creel 2018). Researchers must understand a species' life history, surrounding habitat, and predator-prey dynamics when evaluating glucocorticoids as an indicator of stressors within an environment (Dantzer et al. 2014).

When measuring stress levels in wild populations, there are several methods to consider including plasma and fecal analysis (Sheriff et al. 2010). Blood samples measure plasma glucocorticoid concentrations within the body, but samples can be difficult to collect and can show inconsistent results when measuring baseline concentrations (chronic stress levels) due to the presence of free glucocorticoids (Sheriff et al. 2011, Dantzer et al. 2014). Fecal samples are a non-invasive method allowing you to reduce additional stress on the species of study caused by the hands-on techniques needed for collecting blood. Fecal samples provide a more accurate indicator of chronic stress because glucocorticoids must first be metabolized in the liver before leaving the body, degrading any free glucocorticoids, and providing a more consistent summary of an individual's physiological condition (Sheriff et al. 2010). With any collection method, there are several factors that can impact glucocorticoid concentrations that must be considered when creating protocols. Hormone levels naturally fluctuate throughout the year due to the body's response to environmental changes and they may change in relation to reproductive status or alter during different times of day (Dantzer et al. 2014). Another key factor in measuring stress levels is the need for species-specific validation to ensure accurate results (Sheriff et al. 2011).

As a commonly hunted prey species, bobwhite provide a unique study on how proactive and reactive behaviors can alter prey demography. Bobwhite must not only evade natural predators, but they must also contend with human hunters. Non-consumptive effects of hunting during the wintering months may influence foraging behavior, survival and body condition leading into the breeding season possibly impacting reproduction and population numbers (Lima 1998). Very few studies have investigated the cascading effects of hunting on bobwhite and to our knowledge, none have used glucocorticoids as an indicator of these effects. This thesis aims to investigate how bobwhite mitigate the stress of hunting through proactive and reactive behaviors and how the consequences of those behaviors influence breeding output. We hope that the results of this study help to provided additional tools for managers, allowing them to gain a better understanding of bobwhite ecology and aid in creating holistic and informative management practices.

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CHAPTER TWO

PROACTIVE AND REACTIVE RESPONSES OF NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*) TO HUNTING PRESSURE [1]

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ABSTRACT

Northern Bobwhite (*Colinus virginianus*) is an important species to many communities across the southeastern United States but have been in decline for the past several decades. As a commonly hunted prey species, it is important to understand how bobwhite respond to increased hunting pressures. We designed an experiment to understand how late season hunting affects bobwhite demographics and anti-predator behaviors using fecal glucocorticoid concentrations, foraging and movement behaviors, survival, and breeding season metrics. Our results show that bobwhite responded to increased interactions with a shotgun through proactive anti-predator behaviors. After one encounter with a discharged shotgun, bobwhite began foraging further from supplemental feed where the risk of encountering a hunting party was the greatest (β = 0.21, 95% Bayesian credible interval: 0.06, 0.36). Bobwhite responded to increased hunting pressure, particularly late season hunting pressure, via reactive responses through increased *f*GCM concentrations (β = 2.18, 95% CI: 0.21 to 4.15) which decreased survivorship in non-harvested individuals (β = -0.42, 95% Bayesian credible interval: -0.77, -0.07) and decreased fecundity (β = -0.17, 95% CI: -0.31 to 0.09). These results can aid in bobwhite management decisions and assist in the recovery of the species.

INTRODUCTION

Prey species are constantly balancing the acquisition of resources with the need for survival (Abramsky et al. 2002). In the presence of predators, prey engage in anti-predator decision making (Lima 1998) and must weigh the risks of foraging, movement, and breeding behavior with the risk of predation (Creel and Christianson 2008, Cleveland et al. 2012). These interactions and reactions create a landscape of fear in which prey species alter their behavior to become more difficult for predators to detect, encounter, or capture (Lima 1998). As prey respond to fear, they may increase anti-predator behaviors when they perceive to be at high risk and engage in other behaviors such as foraging or mating when they perceive to be at lower risk (Cleveland et al. 2012). If prey perceive that they are at a higher risk of predation, they may shift their foraging behaviors and move from a ‘risky’ habitat to refuge habitat (Matassa and Trussel 2011) or make temporal changes to avoid what they perceive to be a ‘risky’ time (McGrath et al. 2018). These types of responses can determine population dynamics such as group size, fecundity, and survival (Quinn and Cresswell 2004).

When engaging in anti-predator behaviors, prey can display proactive or reactive responses (Creel 2018). For instance, according to the predator-sensitive food hypothesis, predators dictate foraging activity and other behaviors of prey species (Sinclair and Arcese 1995). Prey can mitigate threats via proactive responses by temporally or spatially altering foraging and movement patterns to increase their chances of survival (Valeix et al. 2009, McGrath et al. 2018). These antipredator behaviors may relieve the fear of predation, but they may also result in decreased body condition due to trade-offs (Clinchy et al. 2013). If a risk is unpredictable, prey may respond with reactive behaviors. For instance, according to the predator-induced stress hypothesis, exposure to predation risk causes an increase in the secretion of glucocorticoids, a stress hormone (Clinchy et al. 2013). When prey species are exposed to an unexpected threat, corticosterone is released from the adrenal cortex allowing the individual to engage in fight-or-flight. Interactions with a predator or weather events, such as hurricanes, may result in acute hormone increases that do not have long-term impacts on body condition but allow the individual to mitigate stress and engage in behavioral responses (Wingfield et al. 1998, Dantzer et al. 2014). When the levels of risk become too high or occur too often, and the individual resides in a constant state of fear, the stress impacts become chronic, affecting their physiology (Boonstra 2004, Dantzer et al. 2014) . In many cases, these chronic increases in glucocorticoid levels can be measured and used to track stressors within the environment. For example, increased glucocorticoid levels in Cape fur seals (*Arctocephalus pusillus pusillus*) were shown to be strongly associated with great white shark (*Carcharodon carcharias*) predation risk and increased levels in mourning doves (*Zenaida macroura*) were strongly associated with increased predation risk from human hunters (Roy and Woolf 2016, Hammerschlag et al. 2017). This ability to measure the impact of stressors within an environment on prey species can provide a greater understanding of how game species are affected by hunting and how that influences population demographics.

When making anti-predator decisions, game species must not only account for natural predators, but they must also account for human predators. As predators, humans play a key role in creating an anthropogenic landscape of fear in which they influence behavior modification and fitness of prey species (Little et al. 2014, Spitz et al. 2019). These effects can be consumptive or non-consumptive (Atuo and O’Connell 2017). Non-consumptive effects have been shown to impact prey by altering space use and demography through cues obtained during and after an interaction with a predator (Atuo and O’Connell 2017). Prey may store auditory, visual or chemical cues during an attack or interaction (e.g., the discharge of a shotgun during a hunt) that influences future decision making (Fievet et al. 2008, Hermann and Thaler 2014, Curlis et al. 2016). McGrath et al. (2018) found that after four interactions with hunters and their dogs, Northern Bobwhite (*Colinus virginianus*, hereafter; bobwhite) altered their foraging times to avoid temporal risks (McGrath et al. 2018). Understanding how prey perceive threats within their environment and how it affects their physiology and behaviors is an important factor in management decision making.

Bobwhites and other gamebirds are an economic and culturally important species across much of the world. While a significant amount of resources has been devoted to the study of best habitat management practices, little is known about the cascading impacts of hunting on physiology and demographics. We conducted a study to investigate the effects of hunting on the physiology, behavior, and survival of bobwhite. Bobwhite, as a prey species and quarry for hunters, interpret hunters and their dogs as threats, and in turn, exhibit anti-predator behaviors (McGrath et al. 2018). Our goals were to determine the extent to which bobwhites use proactive and reactive behaviors through a combination of indicators including stress hormones (i.e., *f*GCM levels), foraging and other movements, survival, and reproduction (Table 1). We had two primary working hypotheses recently summarized by Creel (2018). First, according to the predator-sensitive hypothesis, animals alter foraging behaviors to reduce predation risk. Under this hypothesis we expected bobwhites to alter their foraging patterns (i.e., distance to known patch of food) in response to increased hunting pressure. This proactive response may result in a decrease in survival due to inhabiting sub-optimal habitat or, it may mitigate the risk of predation by removing the threat (interactions with hunters) and have no impact on survival, if the threat is not severe. Alternatively, according to the predator-induced stress hypothesis, exposure to predation may prompt reactive responses that affect the secretion of glucocorticoids. Thus, we would predict that an increase in hunting pressure would elevate *f*GCM levels, negatively affecting survival and fecundity. By understanding these cascading interactions, we hope to help managers and biologists gain a more holistic understanding of bobwhite physiology and demographics to assist in the development of management regulations.

METHODS

Study Area

Our study was conducted on a private property in central Florida (Figure 1). The ranch was about 6,767 ha with the focus of the study covering about 3,000 ha. The study site was comprised of 68% mesic flatwoods, 19% marshland, and 4% swamps with the remaining 9% encompassing roads, ponds, and planted fields. The flatwoods were primarily pine savannas characterized by slash pine (*Pinus elliottii*), longleaf pine (*Pinus palustris*), saw palmetto (*Serenoa repens*) and wiregrass (*Aristida stricta*). The climate in central Florida is considered sub-tropical with an average rainfall of 66 mm and average temperature of 19˚C during the bobwhite hunting season (October through March) and an average rainfall of 144 mm and average temperature of 27˚C during the bobwhite breeding season (April through September) (National Weather Service 2019).

The ranch was managed for the hunting of bobwhite, Wild Turkey (*Meleagris gallopavo*), and white-tailed deer (*Odocoileus virginianus*). The bobwhite hunting season took place from November through the first week of March each year with a possession limit of 24 bobwhites (Florida Fish and Wildlife Conservation Commission 2019). Habitat management techniques for bobwhites included a two-year burn rotation, mowing, disking, and predator removal. Predator removal via meso-mammal trap and removal methods is a common practice in gamebird management with the aim of reducing predation pressure to aid the growth in population numbers (Coté and Sutherland 1997, Jackson et al. 2018). Supplemental nutrition (feedlines) was provided as an added resource for bobwhites every two weeks with grain sorghum (*Sorghum bicolor*) spread along main roads (at a width of approximately 15m across) within each hunting course from a tractor.

Experimental Design

The study site was split into six experimental plots (Figure 1). Half of the plots were hunted throughout the entire hunting season (November 10, 2018 through February 25, 2019) while the remaining half were only hunted from November through January (treatments were randomly assigned to each plot). The treatment plots (plots where hunting ended early) were hunted a total of four times and the control plots (where hunting occurred throughout the entire season) were hunted a total of six times.

Bobwhite Trapping

Bobwhites were trapped from October 1 to October 23, 2018 using walk-in funnel traps that were pre-baited for two weeks with grain sorghum. Once captured, every individual received a unique metal leg band (National Band & Tag Company) and the age (adult or juvenile based on primary feathers), sex, and mass (grams) were recorded. Individuals weighing ≥ 132 g were eligible for a Very High Frequency (VHF) telemetry collar (Holohil Systems Ltd.). Each VHF collar included an active/inactive signal to determine if an individual was moving at the time of tracking. No more than five collars were deployed in a covey to ensure a representative sample across coveys. Trapping was conducted under FWC Scientific Collection Permit SPGS-17-70.

Bobwhite Movement and Survival Data

Coveys were monitored throughout the hunting season to investigate fine scale daily movements using ‘intensive’ telemetry. Coveys were chosen at random and tracked every 30 minutes from sunrise to sunset four times throughout the hunting season (McGrath et al. 2018). Locations were collected using homing telemetry techniques (White and Garrot 1990) and recorded from approximately 20-30 meters away. Data was documented using personalized schemas in the Avenza Map application with Apple iPads. The date, location (Universal Transverse Mercator, UTMs), covey ID, presence of other tagged individuals, observer, and active/inactive status were recorded along with any additional comments. Bobwhite survival was monitored throughout the hunting season via ‘regular’ telemetry. The location of every individual was recorded twice a week unless the individual was no longer within the study area or could not be located. Locations were collected using the same methods as ‘intensive’ telemetry locations. If an individual was found dead, the collar was retrieved from the field and the cause of death was determined to be an avian, mammalian or reptilian predator, other, or unknown.

Bobwhite Hunting

Data was collected during every bobwhite hunt conducted within the study area. Two dogs were worked at a time and each were fitted with a Garmin Astro GPS collar system. After each hunt, the GPS data was downloaded using DNR GPS and saved as a shapefile. Telemetry locations of collared bobwhites were also recorded during each hunt. The observer rode on horseback or on the hunting buggy being mindful to remain behind the hunting party so as not to influence the direction of the hunt. When a collared bobwhite was within range of the telemetry equipment, the estimated location was recorded using the Avenza Map application on an Apple iPad along with the date, time, location (Universal Transverse Mercator, UTMs), active/inactive status, which other individuals were present at that location, observer, and type of hunting interaction. Hunting interactions were recorded in two groups: encounter type and hunter interface (Appendix A). Hunting interactions were used to determine the number of times each covey interacted with a hunting party (hunting encounters) and the number of times a shotgun was fired into a covey throughout the hunting season (shotgun encounters). Following each hunt, we recorded the total number of bobwhites harvested including sex and age along with any individual identification including leg band ID and/or VHF telemetry collar identification. We also recorded the number of hunters, start and end times, number of horses, and ambient air temperature.

Bobwhite Fecal Sample Collection

Fecal samples were collected from every collared covey within the study area for the 2018-2019 field season. A sample was collected every month during the hunting season including a pre- and post-hunting season sample (six total samples). The observer determined the location of a roost site the night prior to collection using homing telemetry techniques (White and Garrot 1990) and flagged out the location. The following morning, fecal samples were collected from flagged roost sites after the covey dispersed from the roosting area. Each sample was stored in a plastic bag with a label recording the date, time, location (Universal Transverse Mercator, UTMs), observer, unique covey ID, and which other individuals were present at that location. Samples were transported from the field to an on-site chest freezer using small coolers and were stored at ≤ -50˚C. After the field season ended, all fecal samples were transported on dry ice to the University of Georgia and stored at -80˚C until further analysis. Fecal sampling was determined to be the preferred choice for glucocorticoid analysis due to its non-invasive sampling methods, its ability to capture chronic stress levels, and its species-specific validation for the use with bobwhites (Sheriff et al. 2010, 2011, Dantzer et al. 2014, Mohlman et al. 2020).

Fecal Sample Preparation & RIA Analysis

Preparation and analysis of fecal samples took place at the University of Georgia. To prepare samples for analysis, each sample was dried for a minimum of 24 hours in a lyophilzer. Once samples were dried, accounting for water and fiber content, each sample was finely ground to ensure all fecal pellets within a sample were properly mixed and 0.5 g of the sample was weighed and placed into a labeled centrifuge tube. Each sample was then mixed with 1 mL of 90% methanol, vortexed for 30 minutes at 1,600 rpm and centrifuged for 20 minutes at 14,000 rpm. The supernatant (0.8 mL) was then transferred to a glass test tube and dried under air on low heat until the methanol evaporated off the sample, approximately 12 hours.

The *f*GCM levels from each sample were measured using a corticosterone I^{125} radioimmunoassay kit from MP Biomedicals. A total of eight assay were run (seven assays of 30 samples and one assay of 27 samples) for a total of 237 samples. Each assay contained approximately five samples (chosen at random) from every collection round to reduce intra-assay variation and the same controls were used across all assays to reduce inter-assay variation. Prior to running an assay, all materials were removed from refrigeration, brought to room temperature, and reconstituted with 600 µl of the buffer included within each RIA kit. The assays were then run according to the provided protocol in each kit. The coefficient of variation was calculated for inter/intra-assay variations to determine the amount of variation during analysis. The inter-assay variation was calculated at 6.8% and the intra-assay variation was calculated at 9.1%, both of which fall within the acceptable range.

Nesting Data

Nesting data was collected throughout the 2019 breeding season using homing telemetry techniques (White and Garrot 1990). Once an individual was determined to be in the same location twice in a row, a researcher flagged out the location by placing three flags in a triangle approximately five meters apart surrounding the suspected nest. They then returned to the suspected nest when the individual was off the nest to confirm the number of eggs, location (Universal Transverse Mercator, UTMs), date the nest was first detected, and the date the nest was confirmed. Once the nesting site was confirmed, it was observed twice a day to monitor breeding activity. Once the individual left the nest, the fate of the nest was determined to have failed or been a success. If the nest failed, the researcher returned to monitoring the individual twice a week for survival. If the nest was a success, the number of eggs (hatched and unhatched), date of confirmation, and suspected hatch date was recorded, and the brood monitoring protocol began.

Statistical Analysis

Fecal Concentrations

To understand how hunting metrics influenced *f*GCM concentrations, we created a candidate model sets using R Studio (R Core Team 2019) (Table 2). We identified *f*GCM concentrations as the response variable and chose several explanatory variables including the treatment the individual was associated with during the hunting season (hunted throughout the entire season or only hunted from November through January), the number of encounters the covey had with a hunting party up to the point of sample collection, and the number of times the covey encountered a shotgun discharge up to the point of sample collection. We also incorporated a time variable representing the time before the treatment went into effect and after the treatment went into effect and included a null model for comparison. Models were then evaluated using Akaike's Information Criterion (AIC) to determine the model of best fit (Burnham and Anderson 2002). We ranked models using number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight (Burnham et al. 2011). We then further investigated the top candidate models form each model set to explain the driving patterns of the response variables.

Movement Analysis

To understand how hunting pressure influences bobwhite daily movements and foraging behavior, we created 161 trajectories from 'intensive' telemetry locations recorded throughout the hunting season. For each trajectory of 'real' telemetry locations, a correlated random walk was generated using the same starting location, distributions of turning angles, and distances between relocations were derived from the original trajectory. Correlated random walk models can be a used by comparing known trajectories against random trajectories to identify patterns in area-restricted search and turn angles (Kareiva and Shigesada 1983, Bergman et al. 2000, Fauchald and Tveraa 2003). Correlated random walks were generated using the *'NMs.randomCRW'* function in the '*adeHabitatLT*' package in R Studio (R Core Team 2019).

We used first-passage time to determine the spatial scale at which individuals move across the landscape (Fauchald and Tveraa 2003). First-passage time analysis measures the amount of time an individual spends within an area along a chosen path, or trajectory. A circle of a given radius (r) is placed at each point along the trajectory and the amount of time it takes that individual to cross the circle is measured. This is then used to describe the search effort of the individual in that area. The search effort is scale dependent and is impacted by the size of the circle used. To create regularly spaced intervals along the trajectory of recorded locations, I interpolated locations every 30 minutes for each trajectory (Fauchald and Tveraa 2003) using the '*redisltraj*' function ('*adeHabitatLT*' package in RStudio *v*3.4.4) (R Core Team 2019). A series of radii ranging from 5-100 m (every 5 m) were used to calculate first-passage time values for each step length and the mean variance of log-transformed first-passage time for all trajectories was used to determine the appropriate search radius (Byrne and Chamberlain 2012, McGrath et al. 2018). The appropriate search radius was determined to be 15 m, ensuring that the length of the radius was larger than the estimated GPS error for telemetry locations of 10 m.

Determining Foraging Zones

First-passage time (FPT) values represent the amount of time an individual spends, or search effort, within a given area. The longer it takes for an individual to cross the determined radius, the larger the FPT value will be. This is referred to as area-restricted search (Fauchald and Tveraa 2003). Area-restricted search (ARS) can be used to identify foraging behavior by evaluating the FPT values along a given trajectory. To determine the areas in which individuals were foraging, we identified an ARS threshold using the mean FPT value for each unique trajectory (real and CRW) (Figure 2). Any FPT value above that threshold was determined to represent foraging behavior and each threshold was visually inspected to ensure the results were biologically meaningful. Once foraging behavior was assigned to the appropriate locations along the trajectory, unique foraging bouts were identified. Locations above the threshold that fell within one hour of each other were concluded to belong to the same foraging bout and any locations greater than one hour apart were considered separate unique foraging bouts. One hour was chosen to differentiate between foraging bouts because it has biological significance for bobwhite and represents the amount of time needed for bobwhite to digest a full crop (McGrath et al. 2018). The Euclidean distance from each foraging bout to the nearest feedline (supplemental nutrition spread throughout the study area) was calculated using the '*Euclidean Distance*' tool in ArcMap *v10*.7.1 (Figure 3).

Resource Use Analysis

To understand how bobwhite used concentrated food resources, we recorded several different intrinsic and extrinsic factors corresponding to each recorded telemetry trajectory and each correlated random walk trajectory (Lesmerises and St-Laurent 2017). We then used a logistic regression model in a Bayesian framework to determine the effects of each factor on bobwhite foraging behavior and their use of supplemental feed as a resource. We set vague priors for fixed effects with a mean of zero with a small precision of 0.001. We used a random effect for covey to account for individual-specific variation and to avoid pseudo-replication (Muff et al. 2020). We used a normally distributed prior for the random effect with a mean of zero and gamma-distributed precision terms. The model is found below is as follows:

$$\theta_i = \alpha_j + \beta_1 * HUNTSENCOUNTERED_t + \beta_2 * SHOTSENCOUNTERED_t + \beta_3 * FECALLAST_t + \beta_4 * FECALMONTH_t + \beta_5 * DISTBOUT_t + \beta_6 * HUNTSENCOUNTERED_t * DISTBOUT_t + \beta_7 * SHOTSENCOUNTERED_t * DISTBOUT_t + \beta_8 * FECALLAST_t * DISTBOUT_t + \beta_9 * FECALMONTH_t * DISTBOUT_t$$

where $Y_i \sim$ *Bernoulli* (θ_i) is the model likelihood with the following model priors:

$$\alpha_j \sim \text{Norm}(\mu, \tau);$$

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

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

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

For the above model, Y represents the use or pseudo-random status for each location (1 or 0, respectively), i represents each location, j represents each unique covey, t represents the change over time of each occasion, and k represents the fixed effects. The intercept (α) was allowed to vary among coveys (i.e., a random effect) and the other unobserved quantities (β) represented the fixed effects (Table 4). Markov chain Monte Carlo (MCMC) was then used to estimate the posterior distributions. We used three chains of 30,000 iterations per chain with a burn-in of 15,000 iterations and a thinning rate of one. Convergence was evaluated using visual inspections of the MCMC chains and the Gelman-Rubin statistic (R-hat), values below 1.1 were considered acceptable (Gelman et al. 2004). We completed our analysis using the “*jagsUI*’ package in RStudio *v*3.4.4 (R Core Team 2019).

Survival Analysis

To reflect the non-consumptive effects of hunting on bobwhite, we removed any individuals that were harvested during the season prior to survival analysis. To estimate the weekly survival of bobwhites during the 2018-2019 hunting season, we generated a hierarchical model using the '*jagsUI*' package in RStudio *v*3.4.4 (R Development Core Team 2010). We first created weekly capture histories for every individual (17 weeks total) with a zero indicating the individual was determined to have died during that week and a one indicating the individual was recorded. We then created individual covariate matrices to model the effects of *f*GCM concentrations, treatment, plot, time, numbers of hunting encounters, and number of shotgun encounters on survival. To account for missing *f*GCM values (weeks where no fecal sample was collected) we imputed a *f*GCM value based on the mean and SD of the existing concentrations. The survival model was as follows:

$$logit\left(\varphi_{ij}\right) = \alpha_k + \beta_1 * CONC_{ij} + \beta_2 * TREAT_{ij} + \beta_3 * TREAT_{ij} * TIME_{ij} + \beta_4 * HUNTSENCOUNTERED_{ij} + \beta_5 * SHOTSENCOUNTERED_{ij} + \beta_6 * TIME_{ij} + \epsilon_p$$

with the following model likelihood,

$$Z_{ij} \sim \text{Bernoulli}(\varphi_{ij} * Z_{ij-1})$$

For the above model, *Z* represents the survival metric for each occasion, *i* is the index for each individual, *k* represents each unique covey and *j* represents each week of the hunting season. The prior for the random effect of covey id (α_k) was drawn from a normal distribution with a Student-t-distributed mean (μ) and gamma-distributed precision terms (τ_1).

$$\alpha_k \sim \text{Normal}(\mu, \tau_1)$$

The prior for the plot parameter (ϵ_p) was drawn from a normal distribution with a mean of zero and gamma-distributed precision terms (τ_2).

$$\epsilon_p \sim \text{Normal}(0,\tau_2)$$

The prior for each beta parameter (β) was uninformed Student-t-distribution (Table 6).

$$\beta \sim \text{Student's-t}(0,0.01,1)$$

The model fitting for posterior probabilities was completed using the same methods as above in the resource selection modeling.

Reproduction Analysis

To determine which metrics had an effect on nesting success, we created several candidate model sets using R (R Core Team 2019). We identified four model sets with the following response variables; nest incubation initiation day (the first day of incubation for the first nest was considered day 0, and the difference in time for each nest incubated after that was calculated in days) (Table 8), the total number of nesting attempts for each individual (Table 10), number of eggs incubated in each individual's first nest of the season (Table 11), and individual fecundity (Table 12). We then chose several explanatory variables including the *f*GCM concentrations from the final round of fecal samples prior to the start of the breeding season, the treatment the individual was associated with during the hunting season (hunted throughout the entire season or only hunted from November through January), the number of encounters the individual had with a hunting party during the hunting season, and the number of times the individual encountered a shotgun discharge. We also incorporated a time variable representing the time before the treatment went into effect and after the treatment went into effect and included null models for comparison. Models were then evaluated using Akaike's Information Criterion (AIC) to determine the model of best fit (Burnham and Anderson 2002). We ranked models using number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight (Burnham et al. 2011). We then further investigated the top candidate models from each model set to explain the driving patterns of the response variables.

RESULTS

A total of 497 unique individuals were captured during the 2018 trapping season, of which, 204 received a VHF telemetry collar (approximately 35 bobwhites per plot). Of those 204 individuals, there were 67 confirmed mortalities; 15 from avian predators, 11 from mammalian predators, 21 were harvested, and 20 died from an unknown cause. The hunting season occurred from November 10, 2018 to February 25, 2019 and a total of 285 bobwhites were harvested including 25 collared individuals (including those from previous years, which were not incorporated into the analysis) and 18 banded individuals. Some individuals were encountered more than once on a hunt, resulting in the total number of hunting encounters per covey ranging from one to eight and the total number of shotgun encounters ranging from zero to three. A total of 243 fecal samples were collected of which six samples were unusable due to insufficient sample weight, leaving 237 samples for analysis. Of the 137 individuals that were not confirmed to have died, at least one nest was confirmed for 50 of the individuals (21 failed and 29 successful). Second nests were confirmed for 19 individuals (9 failed and 10 successful) and third nests were confirmed for 4 individuals (13 failed and one was successful). The first nest of the breeding season of those 50 individuals hatched on April 22, 2019 and the final nest hatched on September 10, 2019.

Fecal Concentrations

The change in *f*GCM concentrations was best explained by the number of hunting encounters and the additive effect of the interaction between treatment and time, explaining 67% of the weight of the model and was the only model with a ΔAICc value less than two (Table 2). Further inspection of the model suggested that hunting encounters had the strongest influence on *f*GCM concentrations ($\beta = 2.18$, 95% CI: 0.21 to 4.15; Table 3) and treatment and time were not supported in the model. The model indicated that as the number of encounters a covey has with a hunting party, the greater the *f*GCM concentration (Figure 4).

Resource Use

Intensive telemetry was conducted from November 5, 2018 through February 28, 2019 and a total of 161 intensive trajectories were recorded for approximately 40 coveys. First passage time values ranged from 304 to 28,596 and the means of each track were used as a threshold to detect foraging behavior (mean values per track ranged from 1,456 to 16,791) (Figure 2). Foraging was detected in all trajectories ranging from one to four foraging bouts per trajectory. The average Euclidean distance from foraging bouts to supplemental feed (feedlines) was 23 m with a minimum distance of zero and a maximum distance of 301 m.

The probability that a bobwhite exhibits foraging behavior decreased as the distance to feedlines increased and *f*GCM concentrations increased (β = -0.028, 95% Bayesian credible interval: -0.124, 0.078; Table 5 and Figure 5). The probability that a bobwhite exhibited foraging behavior decreased as the number of hunting encounters increased and the distance to feedlines increased (β = -0.053, 95% Bayesian credible interval: -0.16, 0.061; Table 5 and Figure 6). The probability that a bobwhite exhibited foraging behavior at a farther distance from the feedline increases as the number of shotgun encounters increased (β = 0.209, 95% Bayesian credible interval: 0.062, 0.359; Table 5 and Figure 7).

Survival

Survival results are reported for birds not directly killed by hunter harvest. Survival was not affected by *f*GCM concentrations ($\beta = 0.01$, 95% Bayesian credible interval: -0.06, 0.11). Survival in hunted areas during February was lower post-treatment than during the months of November through January and compared to areas not hunted during February (Table 7 and Figure 8). The overall survival probability increased as the number of hunting encounters increased (β = 0.08, 95% Bayesian credible interval: -0.52, 0.74) (Table 7 and Figures 9 & 10).

Reproduction

Our first set of models explored the effects of hunting metrics on nest incubation initiation date (Table 8). The top model showed an interaction between *f*GCM concentrations and treatment—it garnered 100% of the model weight with no other models within 2 ΔAICc units. Further investigation showed that increased *f*GCM concentrations were associated with increased delay in incubation initiation date (0.009, 95% CI: 0.006 to 0.012, $P < 0.01$; Table 9). The model also showed an interaction effect and *f*GCM concentrations were more pronounced in plots where late season hunting occurred than in plots where hunting ended at the end of January (Figure 11).

Our second and third sets of models had response variables of total number of nesting attempts and the number of eggs incubated in the initial nests for the season (Tables 10 and 11). For both sets, the null model was the top model with weights of ($W = 0.34$ and $W = 0.41$ respectively). Both sets had a second model with a ΔAICc value less than two, however upon further investigation, the results of those models were not significant.

Our final model set looked at the effects of hunting parameters on individual fecundity in the following breeding season. The top model showed *f*GCM concentrations to have the greatest impact with a weight of 100% and to be the only model with a ΔAICc value less than two (Table 12). These results indicated that fecundity decreased with an increase in *f*GCM concentrations across both males and females ($\beta = -0.01$, 95% CI: -0.02 to 0.00, $P < 0.05$; Table 13 and Figure 12).

DISCUSSION

This study is the first to investigate the non-consumptive effects of hunting pressure and timing on gamebirds using an indicator of physiology (i.e., *f*GCM), survival, and reproduction. We found that late season hunting increased *f*GCM concentrations decreasing the survival for non-harvested individuals, and negatively affected fecundity in the following breeding season. Our results supported the predator-induced stress hypothesis and showed that with increased hunting pressure (number of encounters with a hunting party), bobwhite exhibited a reactive anti-predator response in the form of elevated *f*GCM concentrations (Clinchy et al. 2013). We also found support for the predator-sensitive food hypothesis. Bobwhites exhibited proactive anti-predator behaviors in response to increased encounters with a discharged shotgun (Sinclair and Arcese 1995). After one encounter with a discharged shotgun, bobwhite began to forage further from supplemental feed, a location they likely perceived to be a 'risky' space. Understanding human-induced stressors within the environment will facilitate managers making informed and meaningful decisions germane to consumptive use.

While we did not find the number of shotgun encounters to affect *f*GCM concentrations, it did seem to drive behavioral responses. We found that after a covey was shot into once, it began shifting foraging away from supplemental feed (feedlines). This indicates that bobwhite associated the discharge of a shotgun with predation (via hunters and their dogs) and began to proactively alter their foraging behaviors to relieve the stress of predation. This behavior modification, also seen in elk responses to wolves (Creel et al. 2005), supported our predictions and may have alleviated the fear of predation preventing a chronic increase in stress hormones, explaining why we saw no related measurable increase in *f*GCM concentrations associated with this behavior. This pattern was also detected by Hammerschlag et. al. (2017) in his study of Cape fur seals. Individuals that were able to proactively avoid predators using geographic features while foraging did not show an increase in stress levels whereas individuals that were not able to modify their behaviors saw increases in *f*GCM concentrations with an increase in predation. This behavioral response could be crucial when developing management plans.

Supplemental feed is a common management technique for bobwhite, particularly in sub-optimal habitat or harsh climates when food is a limiting factor (Rosene 1969). If hunter presence along feedlines creates a ‘risky’ space, bobwhite may decide the risk of predation is not worth the nutritional benefits, and temporally or spatially alter foraging (Valeix et al. 2009, McGrath et al. 2018). Reduced use of supplemental feed may result in decreased body condition due to a lack of resources or malnutrition (Clinchy et al. 2013). This consequence would not only negatively affect bobwhite populations, it would devalue the time and monetary cost of spreading supplemental feed.

We also observed reactive anti-predator behaviors. As bobwhite were exposed to an increase in hunting pressure, *f*GCM increased in accordance with the predator-induced stress hypothesis (Sinclair and Arcese 1995). This has been identified in previous studies, specifically, a study in Illinois that recorded measurable increases in *f*GCM concentrations in Mourning doves as a result of hunting pressure (Roy and Woolf 2016). A chronic increase in *f*GCM concentrations can have a variety of consequences and not only affect the survivorship of non-harvested individuals, but impact reproduction (Sinclair and Arcese 1995, Boonstra 2004, Sheriff et al. 2009). This effect was pronounced in late season hunting cascading into the breeding season. By removing hunting in half of the plots during the month of February, we were able to distinguish the natural seasonal changes in hormone levels from the experimental effects. We were able to account for the negative impacts of late season hunting on reproduction with evidence of reproductive suppression and reduced fecundity. Previous research has indicated that individuals experiencing increased stress may prioritize increased vigilance and survival having negative impacts on reproductive success (Lima and Bednekoff 1999, Creel et al.

2007, Sheriff et al. 2009, Ouyang et al. 2012, Yin et al. 2017). Bobwhite exhibited this through a delay in nesting. We observed a delay in nest incubation initiation with increased *f*GCM concentrations where late season hunting occurred. Previous studies on passerines suggest with increased stress-induced corticosterone levels, a glucocorticoid hormone, were more likely to abandon nests prior to the onset of incubation (Ouyang et al. 2012, Vitousek et al. 2014). This could be a factor in the delayed nesting we observed, with the possibility of individuals in hunted plots abandoning earlier nesting attempts. We also observed a decrease in individual fecundity with an increase in *f*GCM concentrations. This could be caused by a decrease in sex hormones (Romero 2004, Creel et al. 2007), or reduced body condition as seen in plateau pikas (*Ochotona curzoniae*) (Yin et al. 2017). Further studies into the consequences of chronic *f*GCM concentrations on bobwhite reproductive output would be required to determine if bobwhites are reducing reproduction due to behavioral or physiological and hormonal changes.

The observation of delayed nesting and reduced fecundity in response to increased *f*GCM concentrations from late season hunting could be particularly useful for hunting regulations and management plans. In Florida, the bobwhite hunting season extends from November 14th to March 7th (Florida Fish and Wildlife Conservation Commission 2019). We observed incubation beginning in the last week of March with hatching starting mid-April, which is supported by previous studies in the area (Singh et al. 2010). This would suggest that bobwhites in central Florida begin reproductive behaviors such as pairing off, nest building, and laying before the hunting season has officially ended (Rosene 1969). By shifting the hunting season to end earlier, managers may be able to reduce late season impacts on reproduction, possibly increasing fecundity.

While our results are substantial and provide keen insight into the cascading impacts of late season hunting on gamebirds, it is important to note that data was only collected from one study year. It would be beneficial for additional research to be conducted over longer periods of time to account for annual variation that may be influenced by larger systems such as weather events or landscape-level dynamics, as well as across the bobwhite range. The impact of shotgun encounters on physiology should also be investigated further. While we detected proactive anti-predator behaviors, we did not detect a significant change in *f*GCM concentrations related to shotgun encounters. This could be the result of mediation through behaviors to relieve predation risk or it could be due to the low number of shotgun encounters. McGrath et. al. (2018) found that bobwhite altered foraging behavior after four encounters with a shotgun discharge, however we only observed a maximum of three encounters. This may indicate a possibility of detecting changes in *f*GCM concentrations with higher shotgun encounters.

In conclusion, bobwhites exhibit proactive and reactive responses when faced with increased late season hunting pressure subsequently affecting reproduction. This research is novel in gamebird management and can be used as an important tool when determining hunting regulations and best management practices. By understanding the consequences of non-consumptive anthropogenic pressures, managers may be able to minimize the negative impacts of late season hunting, increasing fecundity, and as a result, aiding in population recovery. Not only would this benefit the species as a whole, it would improve hunter satisfaction and management efficiency.

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TABLES AND FIGURES

Table 1. How bobwhite will respond to the effects of hunting pressure via proactive and reactive anti-predator responses and how we will measure those responses using foraging behavior, *f*GCM concentrations, survival and fecundity.

Indicator	**Proactive** *Risk is predictable, responses to short- and long-term risk.*	**Reactive** *Risk is unpredictable, responses to short-term risk.*
Foraging	Shift foraging patterns away from areas of 'high' risk to areas of perceived 'lower' risk. Bobwhite will shift foraging further from feedlines as hunting pressure increases.	There will be no changes measured in this study.
*f*GCM	There will be no changes measured in this study.	Concentrations will increase with increased hunting pressure as stressors become chronic. Bobwhites in plots where hunting does not occur (treatment plots) will see a lesser increase later in the season than those that are hunted throughout the study (control plots).
Survival	There will be an increase or neutral response to birds not killed by harvest. The implementation of proactive responses may decrease the threat of predation, mediating the effect on survival.	The negative effects of increased *f*GCM levels as a reactive response may cause a decrease in survival for bobwhites not directly harvested, however later in the season, there will be increased survival for bobwhites in plots where hunting does not occur in February (treatment plots) due to the decrease in predation (hunting) pressure.
Fecundity	There will be no changes measured in this study.	There will be a decrease in reproduction. Increased predation may result in decreased body condition or a reduction in breeding behavior resulting in reproduction decline.

Table 2. Linear model comparisons investigating the effects of hunting season parameters on *f*GCM concentrations during the 2018-2019 bobwhite hunting season. Modeling was completed using the number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight.

Model	**Notation**	**K**	**AICc**	**ΔAICc**	**ML**	**Weight**
hunting encounters + treatment * time	hunt+treat*time	6	2024.98	0.00	1	0.67
treatment * time	treat*time	5	2027.69	2.71	0.26	0.17
shotgun encounters + treatment * time	shot+treat*time	6	2027.88	2.90	0.23	0.16
null	null	2	2037.15	12.17	0.00	0.00

Table 3. Model estimates, standard errors (SE), and 95% confidence intervals from the top ranked model (~hunting encounters + treatment*time) investigating the effects of hunting season parameters on *f*GCM concentrations during the 2018-2019 bobwhite hunting season (Table 2).

Coefficient	**Estimate**	**SE**	**LCL**	**UCL**
intercept	23.38	6.43	10.72	36.04
hunting encounters	2.18	1.00	0.21	4.15
treatnotHunted	5.05	4.55	-3.91	14.02
timebefore	-2.66	5.24	-12.99	7.67
treatnotHunt:timebefore	-1.18	5.38	-11.78	9.43

Table 4. The parameters and their associated effects included in the resource selection logistic regression model.

Parameter	**Effects**
α	The model intercept representing the random effect of each covey.
β_1	The number of times covey *i* interacted with a hunting party prior to the date of the movement data.
β_2	The number of times a firearm was shot into covey *i* prior to the date of the movement data.
β_3	The concentration of the last *f*GCM sample collected for covey *i* prior to the date of the movement data.
β_4	The average concentration of *f*GCM samples collected for covey *i* during the month that the movement data was collected.
β_5	The Euclidean distance (m) between each foraging bout for covey *i* and the nearest feedline.
β_6	The interaction between the number of times covey *i* interacted with a hunting party and the Euclidean distance between foraging bouts for covey *i* and the nearest feedline.
β_7	The interaction between the number of times a firearm was shot into covey *i* and the Euclidean distance between foraging bouts for covey *i* and the nearest feedline.
β_8	The interaction between the concentration of the last *f*GCM sample collected for covey *i* prior to the date of the movement data and the Euclidean distance between foraging bouts for covey *i* and the nearest feedline.
β_9	The interaction average concentration of *f*GCM samples collected for covey *i* during the month that the movement data was collected and the Euclidean distance between foraging bouts for covey *i* and the nearest feedline.

Table 5. Resource selection logistic regression model posterior mean estimates including the mean, standard deviation, 95% Bayesian credible intervals, and probability of detection (the proportion of the posterior distribution that is of the median's sign (Makowski et al. 2019)) for the parameter effects on the probability of foraging for bobwhites during the 2018 - 2019 hunting season. The parameters included the number of hunting encounters, number of shotgun encounters, *f*GCM concentrations, distance to feedline (m), and parameter interactions.

Parameter	**Mean**	**SD**	**2.5%**	**97.5%**	***pd***
μ.use	0.019	0.048	-0.076	0.112	0.653
τ.UniqueID	39.706	15.126	17.442	75.828	1.000
β_1	-0.032	0.051	-0.131	0.068	0.732
β_2	0.052	0.054	-0.055	0.159	0.832
β_3	-0.038	0.044	-0.124	0.048	0.808
β_4	-0.036	0.044	-0.122	0.049	0.795
β_5	-0.191	0.052	-0.293	-0.090	1.000
β_6	-0.053	0.058	-0.166	0.061	0.819
β_7	0.209	0.076	0.062	0.359	0.997
β_8	-0.042	0.054	-0.149	0.065	0.783
β_9	-0.097	0.057	-0.209	0.014	0.956

Table 6. The parameters and their associated effects included in the hierarchical survival model.

Parameter	Effects
α	The model intercept representing the random effect of each covey.
ϵ	The parameter account for each plot within the study.
β_1	The concentration of the last *f*GCM sample collected for covey *i* prior to the date of the movement data.
β_2	The treatment parameter (i.e. whether a plot was hunted in February (control) or if hunting ended at the end of January (treatment).
β_3	The interaction between treatment and time.
β_4	The number of times covey *i* interacted with a hunting party prior to the date of the movement data.
β_5	The number of times a firearm was shot into covey *i* prior to the date of the movement data
β_6	The time parameter (i.e. if it was prior to the implementation of the treatment (November -January) of after (February).

Table 7. Hierarchical model posterior mean estimates including the mean, standard deviation, 95% Bayesian credible intervals, and probability of detection (the proportion of the posterior distribution that is of the median's sign (Makowski et al. 2019)) for the parameter effects on bobwhite survival during the 2018 -2019 hunting season (excluding individuals that were harvested). The parameters included plot, *f*GCM concentrations, treatment, numbers of hunting encounters, number of shotgun encounters, and time.

Parameter	**Mean**	**SD**	**2.5%**	**97.5%**	***pd***
τ.cov	6.88	6.84	0.56	25.31	1.00
τ.plot	6.16	6.21	0.55	23.14	1.00
μ.surv	4.27	1.17	2.17	6.69	1.00
ϵ.plot[1]	0.06	0.50	-0.93	1.11	0.54
ϵ.plot[2]	0.02	0.44	-0.86	0.92	0.51
ϵ.plot[3]	0.22	0.50	-0.67	1.34	0.68
ϵ.plot[4]	-0.25	0.49	-1.35	0.61	0.71
ϵ.plot[5]	0.39	0.47	-0.41	1.45	0.83
ϵ.plot[6]	-0.16	0.52	-1.30	0.82	0.63
ϵ.plot[7]	-0.27	0.43	-1.20	0.53	0.76
ϵ.plot[8]	0.00	0.00	0.00	0.00	1.00
μ.con	27.91	0.00	27.91	27.91	1.00
τ.con	0.00	0.00	0.00	0.00	1.00
sd.con	16.99	0.00	16.99	16.99	1.00
β_1	0.01	0.05	-0.06	0.11	0.55
β_2	-1.45	0.70	-2.91	-0.13	0.98
β_3	2.64	0.93	0.90	4.59	1.00
β_4	0.08	0.32	-0.52	0.74	0.59
β_5	0.49	0.20	0.12	0.89	1.00
β_6	-3.38	0.88	-5.17	-1.73	1.00

Table 8. Generalized linear model comparisons from a Poisson distribution investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on the nest incubation initiation at the start of the following breeding season. Modeling was completed using the number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight.

Model	**Notation**	**K**	**AICc**	**ΔAICc**	**ML**	**Weight**
*f*GCM concentration * treatment	conc*treat	4	782.50	0.00	1.00	1.00
*f*GCM concentration + treatment	conc+treat	3	798.15	15.65	0.00	0.00
*f*GCM concentration	conc	2	805.25	22.75	0.00	0.00
treatment	treat	2	816.03	33.53	0.00	0.00
shotgun encounters	shot	2	826.43	43.93	0.00	0.00
hunting encounters	hunt	2	827.50	44.99	0.00	0.00
null	null	1	828.13	45.62	0.00	0.00

Table 9. The log model estimates, standard errors (SE), and 95% confidence intervals (2.5% and 97.4%) from the top ranked model (~*f*GCM concentration * treatment) investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on the nest incubation initiation at the start of the following breeding season (Table 8).

Coefficient	**Estimate**	**SE**	**LCL**	**UCL**
intercept	3.504	0.074	3.581	3.647
lastConc	0.009	0.001	0.006	0.012
treatmentnotHunted	0.233	0.101	0.035	0.430
lastConc:treatmentnotHunted	-0.009	0.002	-0.013	-0.005

Table 10. Generalized linear model comparisons from a Poisson distribution investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on the total number of nests laid during the following breeding season. Modeling was completed using the number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight.

Model	**Notation**	**K**	**AICc**	**ΔAICc**	**ML**	**Weight**
null	Null	1	103.87	0.00	1.00	0.34
*f*GCM concentration	conc	2	103.96	0.09	0.96	0.32
shotgun encounters	shot	2	105.97	2.11	0.35	0.12
treatment	treat	2	106.06	2.20	0.33	0.11
hunting encounters	hunt	5	106.08	2.21	0.33	0.11

Table 11. Generalized linear model comparisons from a Poisson distribution investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on the number of eggs incubated in the first nest of the following breeding season. Modeling was completed using the number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight.

Model	**Notation**	**K**	**AICc**	**ΔAICc**	**ML**	**Weight**
null	null	1	194.58	0.00	1.00	0.41
treatment	treat	2	196.31	1.73	0.42	0.17
*f*GCM concentration	conc	2	196.76	2.18	0.34	0.14
shotgun encounters	shot	2	196.76	2.18	0.34	0.14
hunting encounters	hunt	2	196.78	2.21	0.33	0.14

Table 12. Generalized linear model comparisons from a Poisson distribution investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on individual fecundity for the following breeding season. Modeling was completed using the number of free parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), delta Akaike's Information Criterion corrected for small sample size (ΔAICc), the model likelihood (ML) and model weight.

Model	**Notation**	K	**AICc**	**ΔAICc**	**ML**	**Weight**
*f*GCM concentration+sex	conc+sex	3	553.55	0.00	1.00	1.00
*f*GCM concentration*treatment	conc*treat	4	593.07	39.52	0.00	0.00
shotgun encounters	shots	2	622.30	68.75	0.00	0.00
null	null	1	623.47	69.92	0.00	0.00
treatment	treat	2	625.43	71.88	0.00	0.00
hunting encounters	hunts	2	625.53	71.98	0.00	0.00

Table 13. The log model estimates, standard errors (SE), and 95% confidence intervals (2.5% and 97.4%) from the top ranked model (~hunting encounters) investigating the effects of hunting season parameters and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on individual fecundity for the following breeding season (Table 12).

Coefficient	**Estimate**	**SE**	**LCL**	**UCL**
intercept	1.15	0.16	0.84	1.45
concentration	-0.01	0.00	-0.02	0.00
sexM	-1.04	0.18	-1.40	-0.70

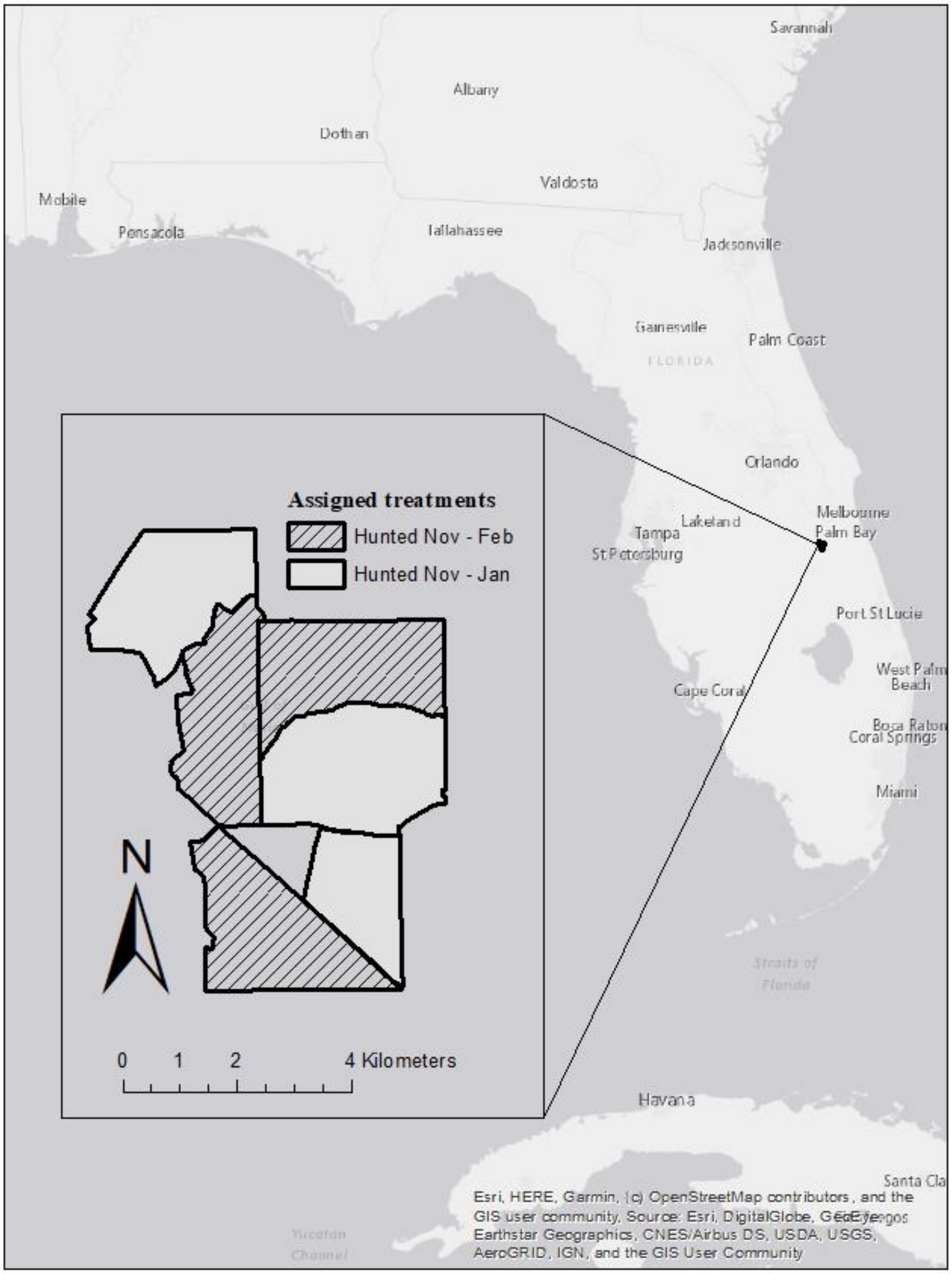

Figure 1. Location of the study site in central Florida, USA. The study was comprised of six plots with randomly assigned treatments. Half of the plots were the control plots and were hunted throughout the entire bobwhite hunting season, November 2018 - February 2019 and the other half were the treatment plots which were only hunted from the months of November 2018 - January 2019.

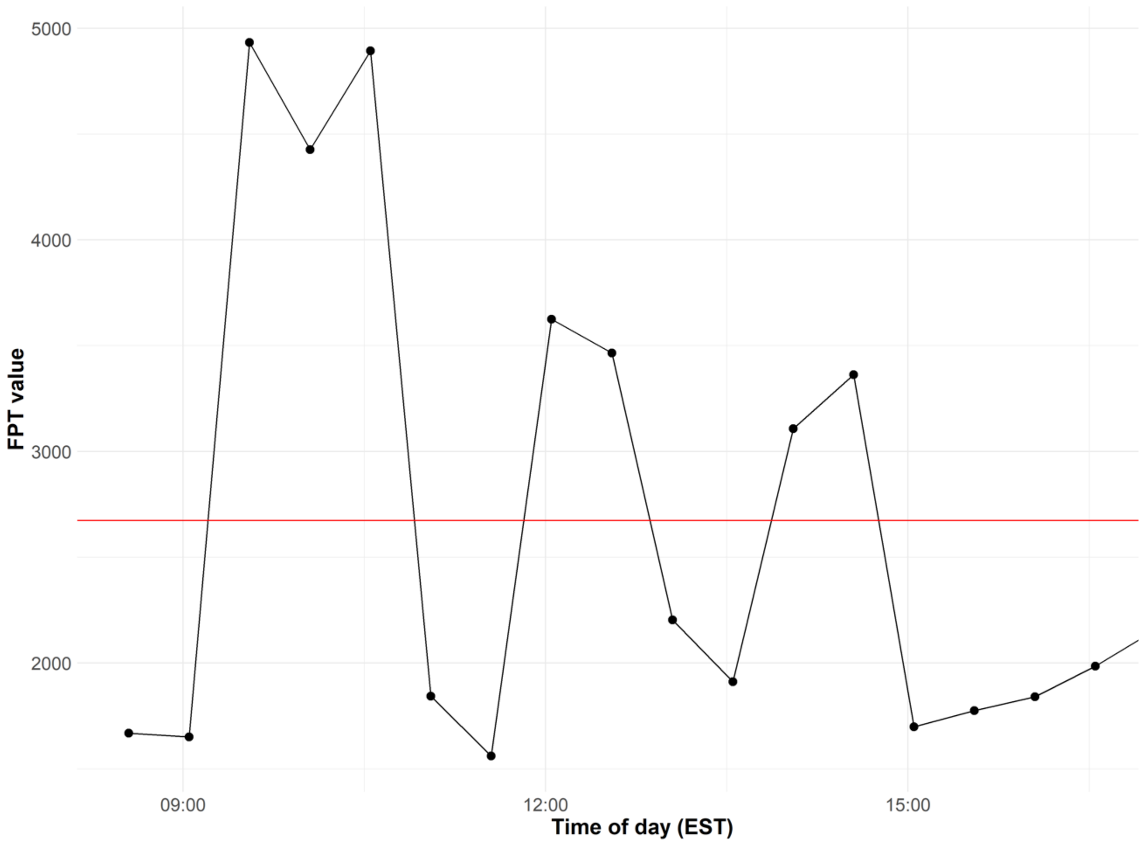

Figure 2. An example of methods used to identify foraging behavior. First-passage time (FPT) values for each location within a trajectory were plotted with time of day (EST) along the x-axis. The red line represents the average FPT value for this trajectory and was used to establish a threshold. FPT values located above the threshold were assumed to exhibit foraging behavior. Foraging locations that were greater than one hour apart were considered unique foraging bouts. The above trajectory represents one unique ‘intensive’ telemetry day with three unique foraging bouts.

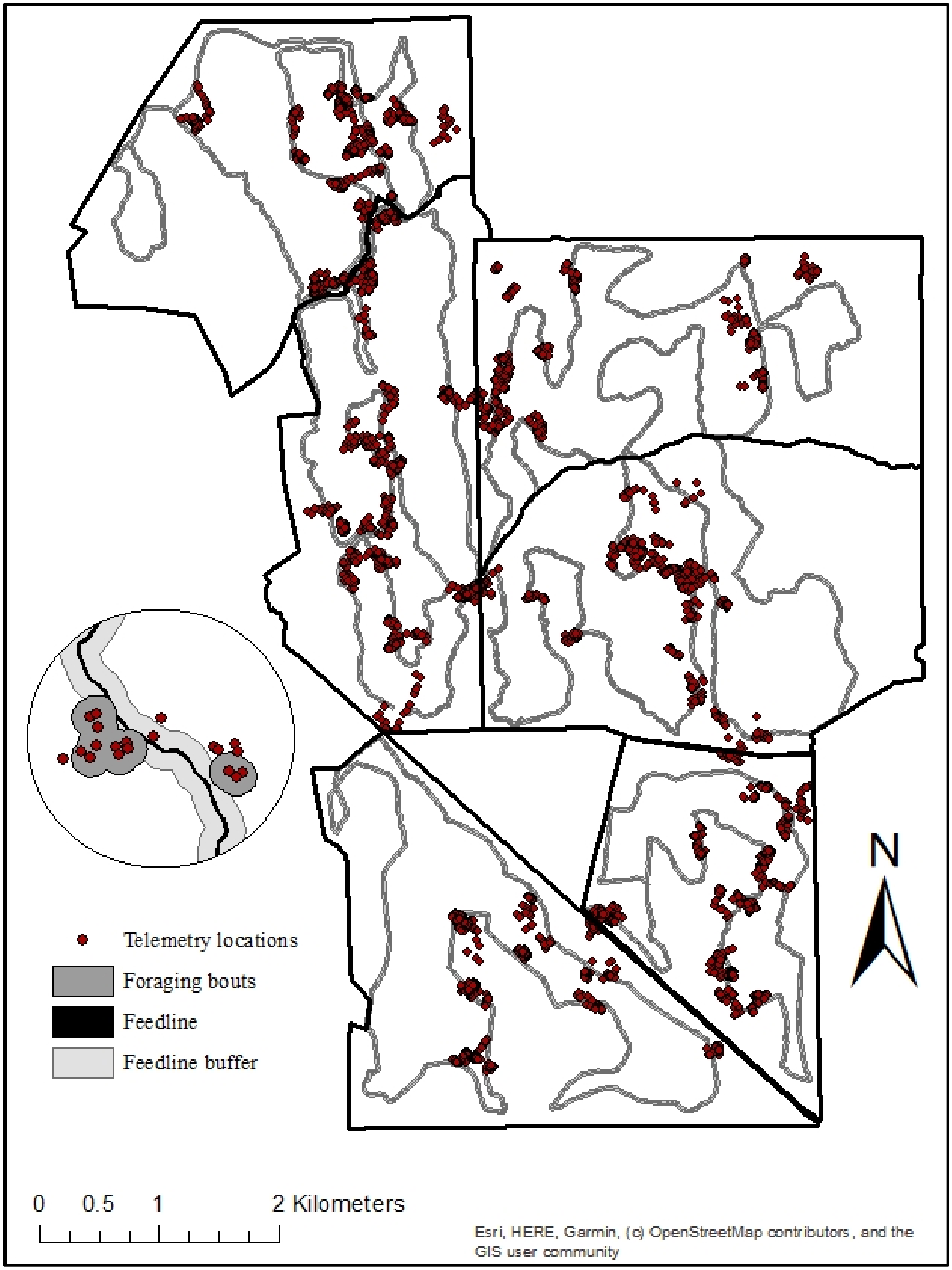

Figure 3. Telemetry locations recorded during ‘intensive’ telemetry throughout the 2018 - 2019 bobwhite hunting season. Foraging locations identified through ARS analysis were buffered to create foraging polygons (foraging bouts). The GPS locations of the feedlines were buffered to 15 m to approximate the actual distance that supplemental feed appears on the landscape.

Figure 4. Results from the top model in Table 2 illustrating the effects of hunting encounters from the 2018-2019 bobwhite hunting season on *f*GCM concentrations.

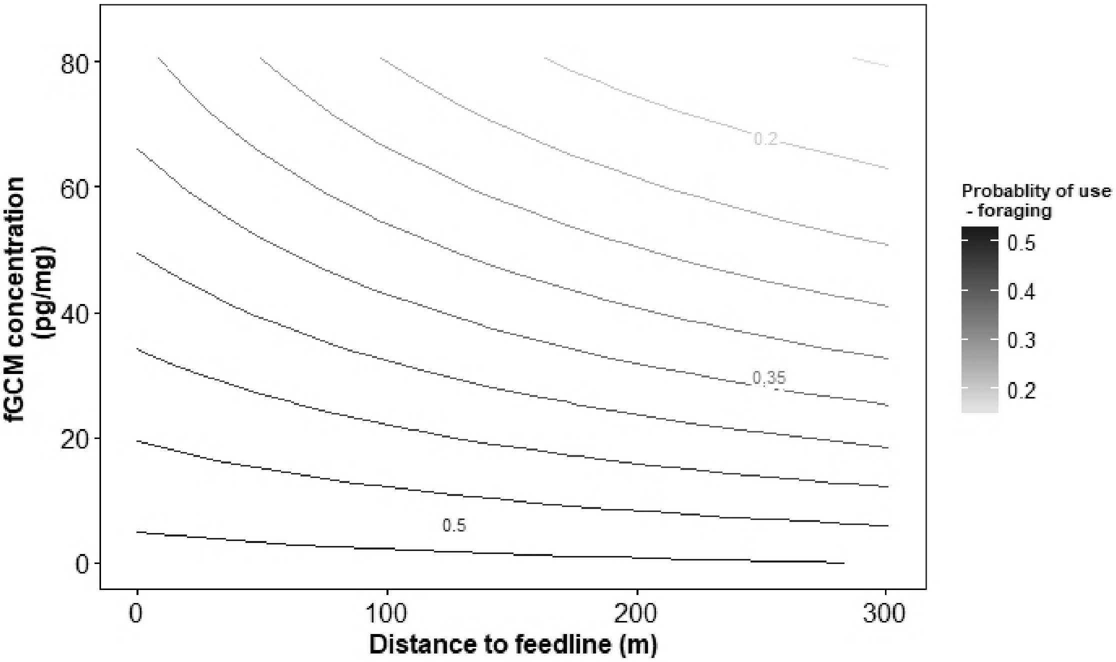

Figure 5. Probability of northern bobwhite expressing foraging behavior in relation to varying *f*GCM levels and the covey's distance from supplemental feed (i.e. feedline). The *f*GCM levels were extracted from fecal samples taken directly prior to the collection of movement data.

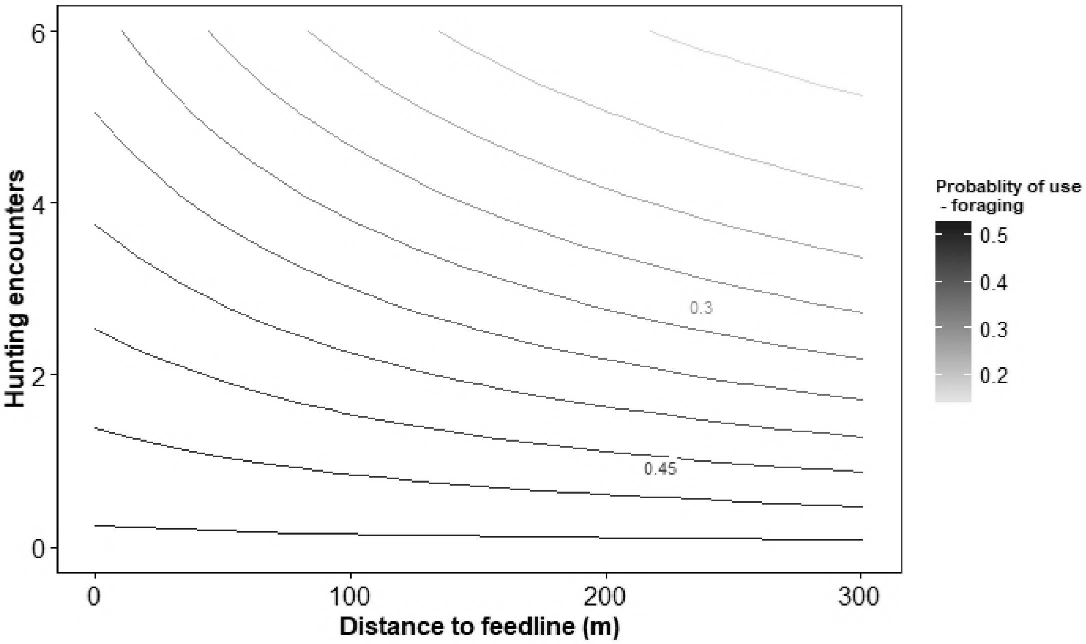

Figure 6. Probability estimates that a bobwhite is expressing foraging behavior in relation to the number of encounters a covey has with a hunting party and the covey’s distance from supplemental feed (i.e. feedline, meters).

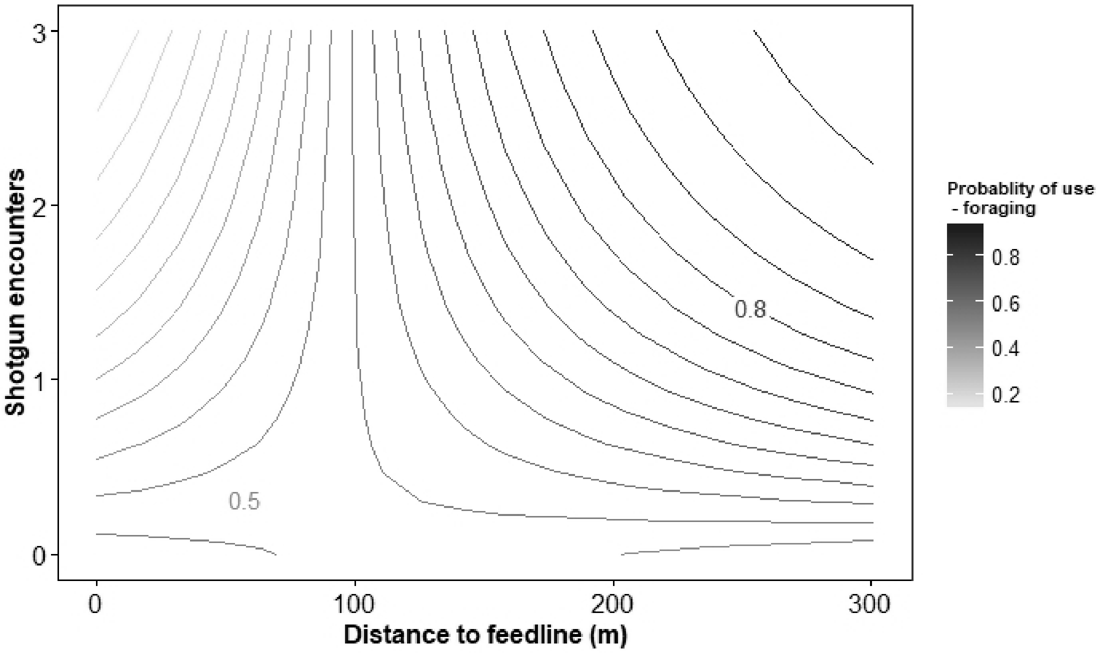

Figure 7. Probability estimates that a bobwhite is expressing foraging behavior in relation to the number of shotgun encounters (the number of times a shotgun was fired into a covey during a hunt) and the covey's distance from supplemental feed (i.e. feedline, meters).

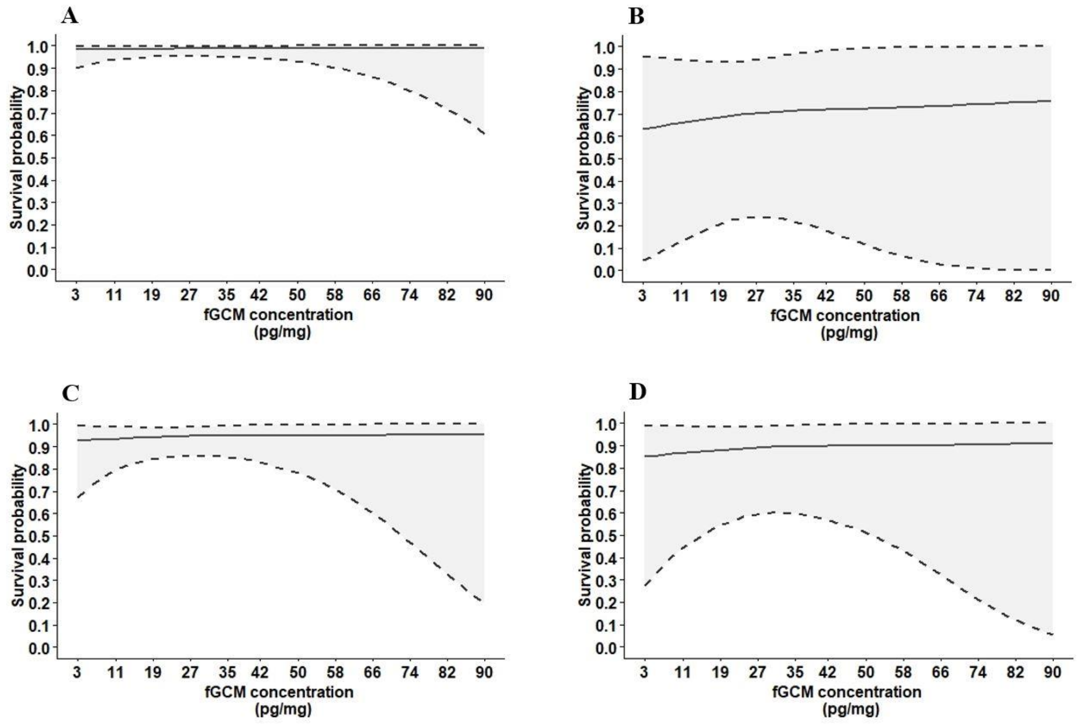

Figure 8. Survival probability estimates of bobwhites across *f*GCM concentrations during the 2018 - 2019 hunting season broken down over time and by treatment. Graphs A and B represent survival probabilities in plots where hunting took place throughout the entire season (control plots) with A representing the months of November through January and B representing the month of February. Graphs C and D represent the survival probabilities in the plots where hunting was stopped at the end of January and no hunting took place during the month of February (treatment plots). Graph C represents the months November through January and graph D represents the month of February.

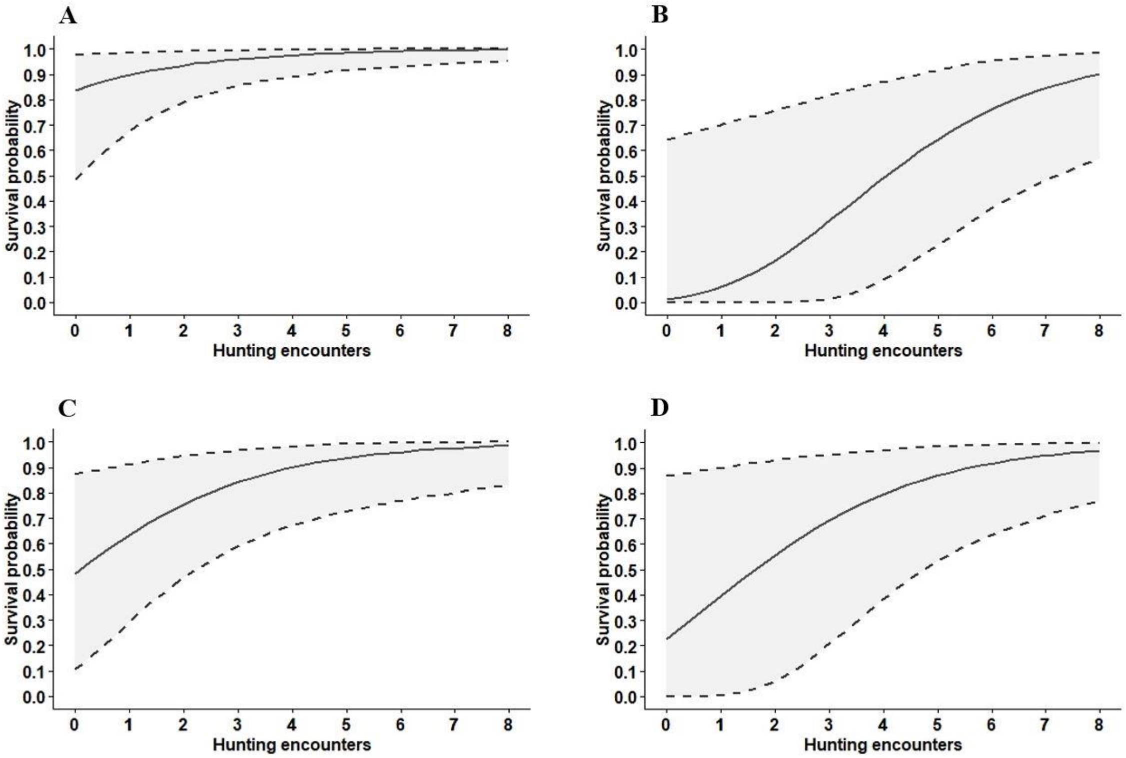

Figure 9. Survival probabilities for bobwhite during the 2018 - 2019 hunting season in relation to the number of encounters with a hunting party broken down over time and by treatment. Graphs A and B represent survival probabilities in plots where hunting took place throughout the entire season (control plots) with A representing the months of November through January and B representing the month of February. Graphs C and D represent the survival probabilities in the plots where hunting was stopped at the end of January and no hunting took place during the month of February (treatment plots). Graph C represents the months November through January and graph D represents the month of February.

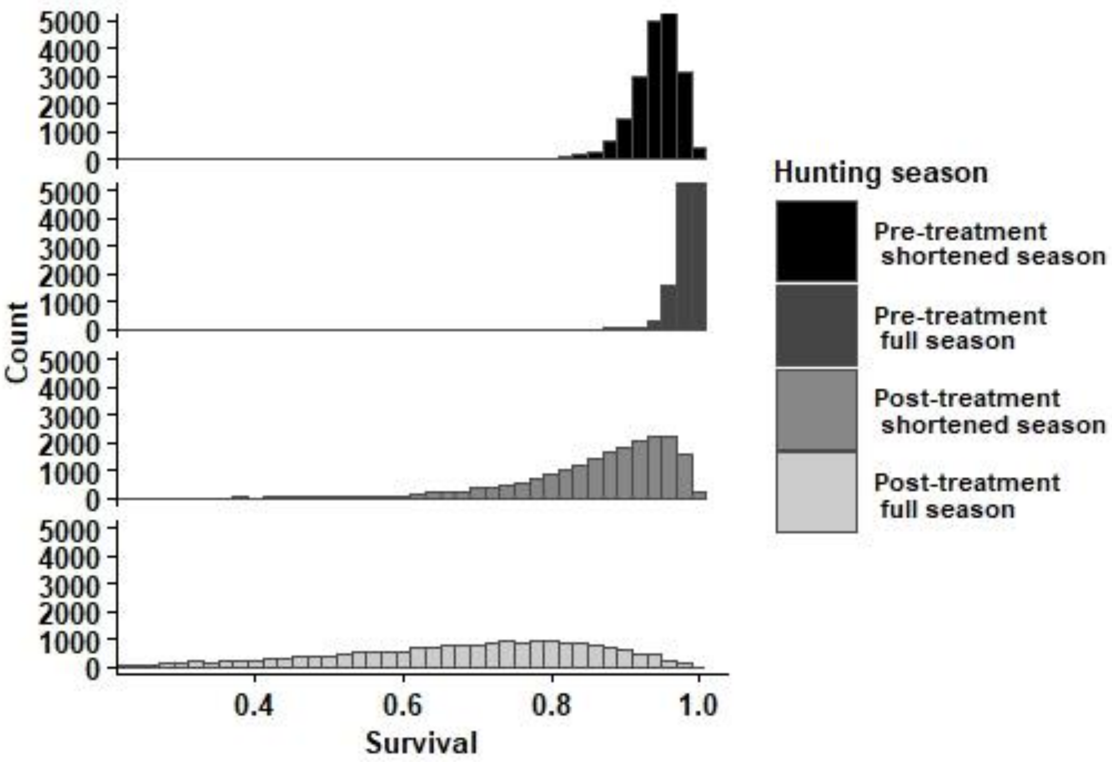

Figure 10. Survival probability for bobwhite across treatments. The top graph represents survival during the months of November-January in plots where hunting ended early , the second graph from the top represents survival during the months of November-January in plots where hunting occurred during the entire season, the second graph from the bottom represents survival during the month of February in plots where hunting ended in January, and the graph on the bottom represents survival during the month of February in plots where hunting occurred during the entire season .

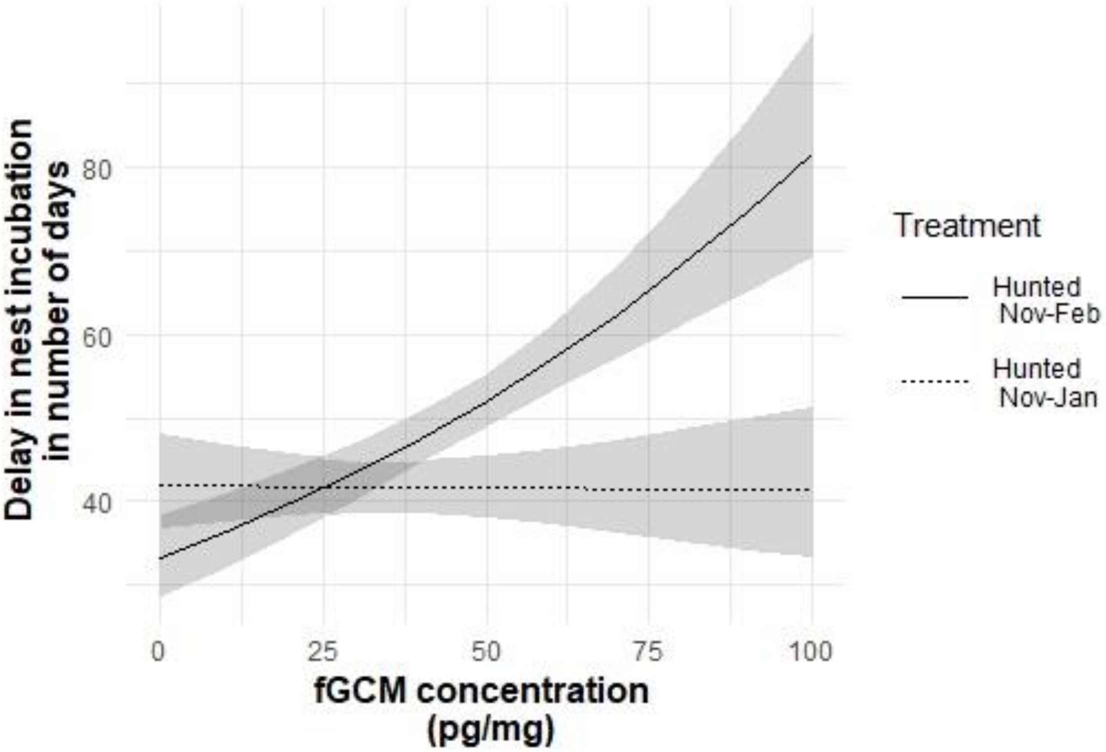

Figure 11. Results from the top generalized linear model in Table 8 illustrating the effects of *f*GCM concentrations and treatment on nest initiation date of the first nest of the 2019 breeding season. The effect of *f*GCM concentrations was compounded in plots that were hunted later in the season than those where hunting ceased at the end of January.

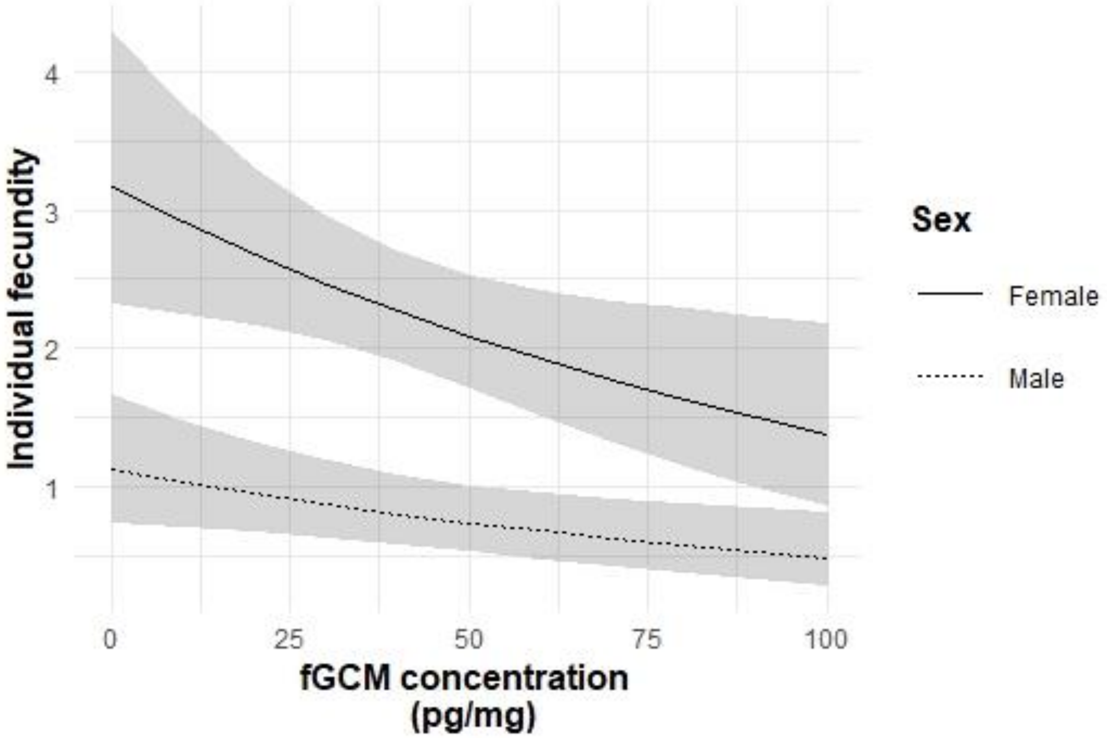

Figure 12. Results from the top generalized linear model in Table 12 illustrating the effects of sex and *f*GCM concentrations from the 2018-2019 bobwhite hunting season on individual fecundity of the following 2019 breeding season. The results of the model indicated that *f*GCM concentrations had the strongest effect on individual fecundity with fecundity decreasing as concentrations increased in both males and females.

CHAPTER THREE

MANAGEMENT IMPLICATIONS

The goal of this study was to determine how bobwhite respond to hunting pressure, specifically late season hunting pressure. We used *f*GCM concentrations, movement and foraging patterns, survival analysis and breeding season metrics to understand how hunting influences demographics. This thesis showed that bobwhite respond to hunting pressure through proactive and reactive responses. Bobwhite proactively responded to increased encounters with a discharged shotgun by foraging further from supplemental feed (where hunters were usually encountered). This proactive behavior may have reduced the fear of predation resulting in no measurable change in *f*GCM concentrations. While this behavioral modification did not seem to influence survival, the climate and surrounding habitat may have played a role. Our study site was on the southern end of the species' range and had relatively mild winters, therefor the reduced use of supplemental feed may not have had a detrimental impact on foraging and nutrition. However, if this behavior modification were to happen in the northern part of the range where winters are harsh and food resources become limited, the consequences of reduced foraging may be much steeper. It could also change the way bobwhite make decisions. If food resources were scarcer, they may decide the benefits of the supplemental feed outweighs the risk of predation. In this case, you may not see a behavioral change, but a physiological one in the form of increased *f*GCM concentrations. It may be possible to reduce the impacts of hunting on supplemental feed use by altering hunting patterns or designating no-hunting zones along different parts of the feedline. By evaluating bobwhite responses, you can understand how they view the landscape and make informed management decisions.

Bobwhite did respond to increased hunting pressure through reactive responses seen in an increase in *f*GCM concentrations. This increase in stress levels did not impact survival, however it did result in delayed nesting and reduced fecundity. Managers and biologists can utilize this information when setting season lengths or timing. We suggest altering the bobwhite hunting season in central Florida either by reducing hunting in the later part of the season or shifting the season to end earlier. Through these actions, managers may be able to increase breeding season productivity aiding in increased population numbers.

This information can be used to provide an important insight into the cascading impacts of hunting pressure and how it may influence bobwhite demographics. Bobwhites are an import gamebird in the southeastern United States and have been the focus of intensive management practices. We believe that our study shows the valuable tool *f*GCM concentration analysis can provide in understanding how bobwhite interact with and respond to their surrounding environments. By integrating this knowledge into management practices, biologist and managers can make informed decisions on hunting regulations and aid in the conservation of the species increasing hunter satisfaction.

APPENDIX A. Description of the different parameters collected during interactions between a hunting party and bobwhites.

Hunter Interaction Type	**Classification**	**Description**
Encounter Type	Covey Point	The dogs pointed a covey.
	Single Point	The dogs pointed a single individual.
	Unproductive	The dogs signaled a point, but no birds were detected by the hunting party.
	Wild Flush	A covey flushed independently of the hunting party.
	Covey Not Detected	A covey was detected to be present by the researcher but was not detected by the hunting party.
Hunter Interface	Shot & Seen	A shot was fired into a covey, but no birds were harvested.
	Not Shot/Seen Only	A covey was seen, but no shots were fired.
	Missed (covey evades hunter/not seen)	A covey was detected to be present by the researcher but was not detected by the hunting party.
	Shot & Harvested	A shot was fired into a covey, and at least one individual was harvested.
	Simulated Shot	A shot was fired into the air, but not into a covey to simulate an active hunt without harvesting an individual.