FORAGING BEHAVIOR, SOCIAL INTERACTIONS, AND PREDATION RISK
OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) AT A
CONCENTRATED RESOURCE

by

DAVID BLEDSOE STONE

(Under the Direction of KARL V. MILLER)

ABSTRACT

Wildlife feeding is undertaken for a variety of reasons including increasing viewing opportunities, improving body condition, preventing starvation, and facilitating hunter harvest. I investigated anti-predator and foraging behavior at bait sites, the role of competition on bait site visitation, and spatio-temporal responses to baiting. During 2013 and 2014, I used global positioning system (GPS) telemetry and camera traps to assess white-tailed deer (*Odocoileus virginianus*) behavior at bait sites and implications for harvest susceptibility. Camera trap data indicated that foraging behavior was influenced by social interactions and breeding chronology. Co-occurrence of mature and immature males at a bait site negatively impacted feeding rates for immature males. I used a multi-state modeling approach to determine if deer temporally partitioned their use of bait sites based on dominance status and how the resulting patterns in bait site visitation would potentially expose deer to different sources of predation risk, depending on the activity patterns of the predator. I found that subordinate (yearling males and adult females) and dominant (adult males) cohorts avoided each other temporally at the patch level. Subordinates were more likely to use bait sites during diurnal hours during the pre- and post-
breeding phases of the breeding season than dominants. Bait site visitation for dominants and subordinates did not differ during nocturnal hours in any phase of the breeding season. Lastly, I used dynamic Brownian bridge movement models and camera traps to assess harvest susceptibility. I determined that hunters were less likely to encounter a deer at a bait site than non-baited areas in their home range, regardless of sex, age class, or phase of the breeding season. Although no sex-age class selected for bait sites over other portions of their home range during legal hunting hours, adult females were more susceptible to harvest at bait sites during the pre-breeding season than the breeding or post-breeding seasons. Conversely, adult and yearling males were more likely to visit a bait site during hunting hours in the post-breeding season than the pre- or breeding seasons. Social interactions, competitive status, and reproductive behaviors are important drivers of deer behavior and harvest susceptibility at bait sites.

INDEX WORDS: baiting, competition, foraging behavior, Georgia, *Odocoileus virginianus*, predation risk, social interactions, vigilance, white-tailed deer
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DEDICATION

This dissertation is dedicated to my wife, Suzanne Stone, for her constant support and inspiration. At the beginning of my academic career, I was unsure of my exact career path. I was deciding between pursuing a medical degree or following my dream and becoming a wildlife biologist. Suzanne insisted that I choose the career that would make me happier. I will always be grateful to her for caring more about my happiness than money. Hopefully, she still feels the same way.
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INTRODUCTION

The white-tailed deer (hereafter: deer, *Odocoileus virginianus*) is the most economically important wildlife species in North America (Schaefer and Main 2001). In Georgia, for instance, deer hunting has an economic impact of > $800 million (Georgia Department of Natural Resources 2004). Conversely, deer also have adverse economic impacts through damage to agricultural crops, disease spread, and deer-vehicle collisions (Romin and Bissonette 1996, Vercauteren et al. 2006). Depending on their abundance relative to the habitat capacity, deer may also affect the distribution or abundance of other species as well as structure of plant and animal communities through direct and indirect competition for resources (McShea and Rappole 1992, Waller and Alverson 1997). Due to the economic and ecological importance of deer, sound management of deer populations is imperative to satisfying the objectives of a diverse group of stakeholders.

Feeding wildlife is a widespread practice (Brown and Cooper 2006, Putman and Staines 2004, Robb et al. 2008) and likely has been for centuries (Inslerman et al. 2006). Providing supplemental feed is particularly common for ungulates in Europe and North America (Brown and Cooper 2006, Putman and Staines 2004). Game managers supplementally feed ungulates for a variety of reasons including increasing winter survival, maintaining high densities, reducing damage to agriculture and forestry, increasing carrying capacity, enhancing juvenile survival,

Wildlife feeding can impact numerous trophic levels (Waller and Alverson 2007) and affect predation rates (Dunn and Tessaglia 1994, Morris 2005), intensify inter- and intra-specific competition (Pimm et al. 1985, Raman 1996), increase disease transmission (Sorensen et al. 2014), alter non-target species behavior and vital rates (Prange et al. 2004, Pedersen et al. 2007, Selva et al. 2014), and reduce habitat quality for both target and non-target species. (Cooper et al. 2006, Robb et al. 2008, Milner et al. 2014). Due to these concerns, some biologists, hunters, and the non-hunting public may disapprove of feeding wildlife, especially as a means to aid game harvest (Pacelle 1998, Michigan Department of Natural Resources 1999).

In the southeastern U.S., supplemental feeding and/or baiting is permitted for at least a portion of the year in every state and baiting as a means to attract deer for harvest is legal in most (Southeast Deer Study Group 2012). Beginning in 2011, hunting deer over bait was legalized in the Southern Zone of Georgia, raising concerns about the effects it may have on deer behavior and harvest susceptibility. Consequently, the Georgia Department of Natural Resources (GADNR) requested the University of Georgia conduct this study to inform future harvest regulations.

LITERATURE REVIEW

Supplemental Feeding and Baiting Definitions

Supplemental feeding is the practice of providing concentrated food for wildlife for the purposes of increasing survival (adult and neonate), nutritional carrying capacity of the habitat, body mass, fecundity, and/or antler size (Ozoga and Verme 1982, Zaiglin and DeYoung 1989, Bartoskewitz
et al. 2003, Page and Underwood 2006). Baiting is the act of providing a food source to attract wildlife for harvest (Kilpatrick et al. 2010), facilitate research objectives (Kilpatrick and Stober 2002), or provide wildlife viewing opportunities (Corcoran et al. 2013). Although they differ in their stated goals, supplemental feeding and baiting share many of the indirect ecological effects that are inherent with providing a concentrated resource.

**Benefits of Supplemental Feeding**

Supplemental feeding programs aim to improve performance at the individual and population levels (Milner et al. 2014). Often, supplemental feeding is used to provide additional nutrition for game species and species that are threatened or endangered (Bartoskewitz et al. 2003, Avizanda et al. 2016). Ungulates, in particular, are fed during times of nutritional stress or as an emergency measure to prevent starvation.

Winter feeding of ungulates is a widespread practice in Europe and North America. In Europe, the practice is so well-engrained into wildlife management that it is mandated by law in Germany, Hungary and Austria (Putman and Staines 2004). Winter feeding aims to decrease mortality, maintain or increase body weight and condition, improve reproductive parameters, and reduce damage to agriculture and forestry (Putman and Staines 2004, Milner et al. 2014). Winter feeding has been successful at improving survival rates and body condition for several ungulate species (Smith and Anderson 1998, Peterson and Messmer 2007, Timmons et al. 2010). For example, white-tailed deer fawn and elk (*Cervus elaphus*) calf survival may increase with supplemental feeding (Lewis and Rongstad 1998, Smith and Anderson 2008). In addition, winter feeding can improve survival, body condition, and reproductive performance of adults (Peterson and Messmer 2007).
Feeding during other times of the year can also lead to improved performance. For example, Ozoga and Verme (1982) reported a long-term supplemental feeding program increased antler size and population density for a captive white-tailed deer herd. Likewise, antler size and body mass may increase for free-ranging deer in some instances (Bartoskewitz et al. 2003).

Supplemental feeding may reduce damage to agriculture, decrease deer-vehicle collisions, and minimize the negative impacts of herbivory (Schmitz 1990, Rajský et al. 2008, Kowalczyk et al. 2011). Diversionary feeding, or intercept feeding, may be an effective tool to redistribute ungulate populations away from roads and regenerating forests (Sahlsten et al. 2010). However, the efficacy of diversionary feeding at reducing human-ungulate conflicts is unclear (Milner et al. 2014).

**Effects of Feeding and Baiting on Disease Transmission and Non-target Species**

There is increasing evidence that feeding can have indirect effects at many trophic levels (Brown and Cooper 2006, Milner et al. 2014). Indirect effects include depredation of non-target species nests (Selva et al. 2014), increased disease transmission (Miller et al. 2003, Admasu et al. 2004), alteration of population dynamics (Martínez-Abraín and Oro 2013), and increased predation of non-target species near baiting and feeding sites (Cortes-Avizanda et al. 2016). These unintended ecological consequences have caused controversy among stakeholders on the merits of providing concentrated resources.

Feeding sites may increase disease transmission through artificially aggregating wildlife leading to increased contact rates (Miller et al. 1998). The role that these resources play in transmission depends on the biology of the pathogen (Sorensen et al. 2014), animal density, and
the method of feed delivery (Robb et al. 2008). Another issue with artificially inflated densities in the vicinity of feeding and baiting sites is that crowding can increase stress levels leading to reduced immune function and increased disease transmission (Forristal et al. 2012).

Common diseases associated with ungulate feeding include chronic wasting disease (CWD), bovine tuberculosis, bovine brucellosis, and various skin ailments (Sorensen et al. 2014). Recently, CWD has spread across much of North America prompting intensive epidemiological research. The disease can be transmitted through urine, feces, and saliva (Denkers et al. 2013, Sorensen et al. 2014). Waste and saliva deposited at bait sites also increases the transmission of CWD as prevalence of the infectious prion is likely to be higher (Sorensen et al. 2014). Therefore, some states have banned baiting in areas infected with CWD. Some have argued that the role of feeding and baiting sites in disease transmission has not received adequate attention in research, especially in light of recent outbreaks of diseases that threaten many economically and ecologically important wildlife species (Sorensen et al. 2014). Clearly, there is much more to learn on the effects of concentrated resources on disease transmission and this aspect of wildlife management will likely gain increasing attention in the coming decades.

There is a plethora of literature on the negative effects of high-density ungulate populations on tree regeneration, plant community structure, and species composition (Doenier et al. 1997, Stromayer and Warren 1997, van Beest et al. 2010, Crider 2012). Intense browsing by high-density herbivore populations can have detrimental effects on native plant species and can impact numerous trophic levels (deCalesta 1994, Waller and Alverson 1997, Mathisen and Skarpe 2011, Pedersen et al. 2014). For example, plant diversity and vertical structure of forests increases when ungulate herbivory is eliminated or ungulate density is reduced (McShea and Rappole 1992, deCalesta 1994). Bird communities respond positively to a reduction in ungulate
herbivory because over-browsing can reduce species richness and abundance for songbirds that rely on the intermediate shrub layer for nesting (deCalesta 1994, Mathisen and Skarpe 2011). Therefore, artificially inflating ungulate densities through supplemental feeding and baiting can cause trophic cascades affecting both plant and animal communities (deCalesta 1994, Waller and Alverson 1997).

Supplemental feeding of wildlife is typically targeted at a single species or a suite of species. However, many non-target species may also consume the feed (Sánchez-García et al. 2015). In fact, Sánchez-García et al. (2015) reported that non-target species comprised the majority of photographs captured at game bird feeding sites and consumed 67% of the feed. This additional food resource can benefit non-targets but they routinely suffer negative consequences induced by wildlife feeding. Common negative impacts include nest predation, reduction in habitat quality, and ingestion of toxic feed (Hamilton et al. 2002, Brown and Cooper 2006, Selva et al. 2014).

Increased bird and turtle nest predation has been reported in the vicinity of wild boar (*Sus scrofa*) and other ungulates’ feeding sites (Greenwood et al. 1998, Hamilton et al. 2002, Mysterud 2010, Selva et al. 2014). Distance of the nest to the feeder and the duration of feeding predicted the probability of predation in Europe where ungulate baiting is common and widespread (Selva et al. 2014). The mechanism for increased nest predation in the vicinity of ungulate feeding sites is the feed’s attraction of non-target, nest predator species, thereby increasing predator encounter rates. Selva et al. (2014) reported that 82% of all photos at an ungulate bait site were of nest predator species including small mammals, brown bears (*Ursus arctos*), wild boar, and numerous birds.
Indirect Effects of Predators on Prey

Foraging theory predicts animals maximize fitness while minimizing predation risk (Schoener 1971). In the presence of predators, prey species must make foraging decisions that maximize both predator avoidance and energy intake (Lima and Dill 1990, Sonnichsen 2013). Predation risk varies temporally and spatially at multiple scales (Tolon et al. 2009, Sonnichsen 2013). Animals exhibit numerous predator avoidance behaviors including selecting habitats that present a lower predation risk (Bongi et al. 2008), foraging closer to escape cover (Banks et al. 1999), reducing activity (Lima and Dill 1990), increasing vigilance (Liley and Creel 2008), and shifting activity times (Jacob and Brown 2000). Most ecological studies have focused on the spatial aspect of predation risk (Creel et al. 2008). This approach simply assumes animals associate long-term predation risk with certain places and adjust their behavior accordingly by avoiding places of increased predation risk (‘risky places hypothesis’; Creel et al. 2008). Focusing only on the spatial side of predation risk, however, can lead to inferences that do not consider temporal variation in predation risk (Creel and Winnie 2005).

Lima and Bednekoff (1999) proposed the ‘Predation Risk Allocation Hypothesis’ to explain the dynamic nature of predator avoidance and incorporates both the spatial and temporal aspects of predation risk. The foundation of the model is that as predation risk varies over time, the relative amount of effort dedicated to vigilance and foraging are contingent upon the level of risk and the proportion of time that predators are present (Lima and Bednekoff 1999, Ferrari et al. 2009). The model predicts that if predation risk is present for a fixed proportion of time, animals will forage more intensively during the low-risk periods (Beauchamp and Ruxton 2011). Under conditions of sustained, high predation risk, the model makes the counter-intuitive prediction that animals should decrease vigilance during both high- and low-risk situations.
because extended bouts of vigilance would decrease the amount of energy intake to levels that would be detrimental (Ferrari et al. 2009, Beauchamp and Ruxton 2011). In other words, if predation risk is high enough for a long enough period of time, prey will actually decrease their predator avoidance behavior during times of high risk. Finally, Lima and Bednekoff (1999) suggested that prey animals should show the greatest response to high-risk situations when predation risk is brief and infrequent.

Although there is emerging evidence that coyotes (*Canis latrans*) may prey on adult female deer (Chitwood et al. 2014), humans are the primary predators of adult deer throughout most of the southeastern United States. Therefore, most anti-predator behaviors should be directed towards humans during the hunting season and because predation risk varies across the landscape and through time, predator avoidance behaviors should reflect the level of risk associated with certain locations during certain times. Bait sites represent highly profitable patches where deer can obtain much of their energy requirements while minimizing energy expenditure. However, because they are hunted over, they are high-risk locations at which to forage. Thus, deer must balance the reward of a consistently abundant food source with the risk of predation.

Animals may minimize predation risk at concentrated feeding sites by adjusting activity times (Lima and Dill 1990). In a hunted population of roe deer (*Capreolus capreolus*), Sonnichsen et al. (2013) observed that during the hunting season deer were less vigilant at night compared to day. Furthermore, they reported that the amount of time spent feeding was higher during the non-hunting season and night-time during the hunting season compared to day-time hours during the hunting season. Crosmary et al. (2012) compared the arrival times for three African ungulate species at hunted and non-hunted watering holes and found that all three
species shifted their arrival times toward more nocturnal patterns to decrease the risk of encounters with hunters— even when the shift to nocturnal feeding increased their risk of predation to natural predators. Shifting activity times at feeding sites to avoid human hunters is likely a learned behavior and illustrates the behavioral plasticity of hunted species when faced with the threat of predation (Sonnichsen et al. 2013).

Animals can also alter vigilance levels in response to predation risk (Elgar et al. 1984, Crosmary et al. 2012, Cherry et al. 2015). Cherry et al. (2015) experimentally manipulated predation risk at white-tailed deer feeding sites by excluding coyotes. They observed higher feeding rates at sites where predation risk from coyotes was eliminated and a positive relationship between feeding and group size. Comparable findings for other taxa illustrate the role that predator vigilance and group size play at bait sites (Elgar et al. 1984, Elgar 1989, Lashley et al. 2014).

The direct and indirect effects of predation risk at bait sites deserve a more thorough study. In particular, data on fine scale predator search behavior at feeding and baiting sites are lacking. There is ample theoretical literature on the predator-patch quality relationship, but empirical evidence for predator search behavior around concentrated resources is deficient. Likewise, both human and non-human-induced predation rates at bait sites warrants much more research.

**Competition at Concentrated Food Resources**

Competition is one of the most important ecological drivers of animal density and distribution (Cresswell 1998). Understanding the role of competition at concentrated resources is vital to determining the ecological consequences of resource provisioning for wildlife. Some animals can affect the distribution or abundance of other species as well as structure of plant and
animal communities through direct and indirect competition for resources (Waller and Alverson 1997). Ecological theory recognizes many types of competition to explain how species compete for resources. One is exploitation, whereby one animal reduces availability of a common resource to another animal (Carothers and Jaksić 1984). Another mechanism is interference competition and occurs when one organism reduces another’s capacity to utilize a shared resource (Carothers and Jaksić 1984). Competition and predation are often related as the outcomes of competition may affect predation risk (Holt 1977).

Resource partitioning may reduce competition within and among species and occurs on both temporal and spatial scales (Schoener 1974). To reduce the effects of competition, animals may segregate along the dietary, habitat, or time niche axis (Schoener 1971, Schoener 1974, Kronfeld-Schor and Dayan 1999, Kronfeld-Schor and Dayan 2003). Spatial and dietary resource partitioning have garnered most of the focus of ecological studies (Kronfeld-Schor and Dayan 1999) and have been deemed more significant mechanisms of reducing competition than has temporal partitioning (Schoener 1974, Kronfeld-Schor and Dayan 2003). However, temporal resource partitioning is important for maintaining the coexistence of species, or individuals of the same species, that must compete for a shared resource (Ziv et al. 1993, Kronfeld-Schor and Dayan 1999) but the ultimate causes of temporal partitioning are hard to discern. Ziv et al. (1993) investigated temporal partitioning in feeding times of two congeneric species of gerbils. *Gerbillus pyramidum* and *G. allenbyi* are both nocturnal but *G. pyramidum* is active earlier in the night. When *G. allenbyi* was removed, *G. pyramidum* shifted its activity time earlier (when their preferred food is more abundant), suggesting that dominance played a role in their partitioning of activity times.
Alanara et al. (2001) experimentally tested the hypothesis that dominance was responsible for intraspecific temporal resource partitioning in brown trout (*Salmo trutta*). They showed that dominant individuals fed during the most energetically beneficial times and when predation risk was lowest. Furthermore, when energetic demands were greatest, subordinate individuals were forced to feed more during diurnal periods when predation risk was higher. Therefore, within a species, social rank can determine which individuals gain access to limited resources such as concentrated food sources at times that are energetically advantageous and present the lowest predation risk. However, the effects of social rank on intraspecific resource partitioning have not been tested in white-tailed deer.

Different sex-age classes within a species commonly compete for concentrated resources. An individual’s ability to dominate limited resources leads to improved body condition and increased reproductive success (Clutton-Brock et al. 1984, Vervaecke et al. 2005). Dominance hierarchies exist within many species with older and larger animals typically holding higher status over younger and smaller individuals (Tarvin and Woolfenden 1997, Donázar et al. 1999, Michel 2016). In such cases, subordinates can be forced to forage in less profitable patches (Donázar et al. 1999) or utilize the resource when dominant individuals are not present (Schoener 1974, Grenier 1999, Schmidt 1997).

**Effects of Supplemental Feeding and Baiting on Animal Movements**

Planting food plots and baiting and/or supplemental feeding share the common goals of concentrating deer for harvest and increasing the nutritional carrying capacity of the habitat, with the main difference being the degree to which forage is concentrated and the effort used to produce the forage. Supplemental feeding and baiting alter natural foraging behavior (Brown and Cooper 2006, Cooper et al. 2006, Timmons et al. 2010) and movement patterns (Ozoga and
Verme 1982, Schmitz 1990, Kilpatrick and Stober 2002). Optimal foraging theory predicts that animals will increase their fitness by maximizing energy intake when utilizing food sources that require the animal to expend the least amount of time and energy while balancing potential negative feedbacks such as predation risk (MacArthur and Pianka 1966, Schoener 1971, Brown et al. 1999). For large herbivores, supplemental feeding and baiting may enable them to maximize the net “profit” of energy intake by allowing them to meet their nutritional requirements by concentrating movements around a high-quality food source (Murden and Risenhoover 1993, Cooper 2006). In contrast to native forages that may be temporally and spatially limited, when offered *ad libitum* in a consistent location, the presence of supplemental feed and/or bait reduces search time and can make movements more predictable.

Ungulates may concentrate movements around supplemental feeding and bait sites resulting in damage to the habitat for deer and other species, particularly when feed is offered for several years in the same location (Cooper et al. 2006, Milner et al. 2014). Baiting may also affect the distribution of animals on the landscape (Milner et al. 2014). For example, in a high-density herd in Connecticut, Kilpatrick and Stober (2002) concluded that bait sites affected the spatial arrangement of core areas by influencing deer to locate their core areas closer to bait or establishing new core areas nearer bait sites during the hunting season. Likewise, in West Virginia, Campbell et al. (2006) reported deer shifted their geographic-centers-of-activity toward bait sites when made available. Conversely, other studies have reported that feeding did not affect the spatial distribution of white-tailed deer (Webb et al. 2009).

**Predation at Bait Sites**

Baiting can alter natural movement patterns and serve to aggregate prey (Orams 2002, Godbois et al. 2004, Corcoran et al. 2013). Predators respond to predictably aggregated prey by
focusing their activity around the resource (Valeix et al. 2010). For example, Turner et al. (2008) reported that red-tailed hawks (*Buteo jamaicensis*) were found 3x closer to Northern bobwhite (*Colinus virginianus*) supplemental feeding sites than by chance. Mammalian predators often select for habitats containing a feed site as well (Godbois et al. 2004). European lynx (*Lynx lynx*) consistently selected habitats that included roe deer feeding sites (Basille et al. 2009). Additionally, omnivorous predators such as raccoons (*Procyon lotor*) and coyotes may show similar spatial responses to concentrated food resources (Hidalgo-Mihart et al. 2004, Prange et al. 2004).

Information on deer harvest susceptibility at bait sites has shown conflicting results. For example, Wisconsin researchers determined that following a ban on baiting in part of the state, deer harvest declined only 0.1 deer/km² for archers (Van Deelen et al. 2006). Similarly, the Pennsylvania Game Commission reported that there was no increase in harvest for hunters in an area where baiting was temporarily legalized (Fleegle and Rosenberry 2010). In contrast, baiting has led to increased hunter harvest in some instances (Frawley 2002, Kilpatrick et al. 2010).

Natural resource agencies charged with managing overabundant herds in urban-suburban areas have legalized baiting with the intention of reducing densities. Kilpatrick et al. (2010) found that 83% of hunters that used bait and 58% of hunters that did not bait harvested at least one deer. Additionally, they found that hunters using bait harvested 3x more antlerless deer than antlered. Similarly, Ruth and Shipes (2005) reported higher female harvest rates for hunters using bait in South Carolina. There is clearly a need to determine which sex-age class may be more vulnerable to hunter-induced mortality at bait sites, as female survival drives population trajectory.
OBJECTIVES

The objectives of this research were to evaluate the spatio-temporal responses of white-tailed deer to bait in west-central Georgia, and to determine how social interactions and competition affect deer behavior and predation risk at bait sites. My specific objectives were to: 1) investigate factors influencing foraging behavior at bait sites, 2) examine the role that social rank plays in temporal resource partitioning and how resulting activity patterns affect predation risk, and 3) determine if deer are more susceptible to harvest at bait sites than other portions of their home range.

DISSERTATION FORMAT

This dissertation is presented in manuscript format. Chapter 1 is an introduction and literature review of relevant studies related to our research topics. Chapter 2 presents the results of an investigation of how breeding chronology, social interactions, and abiotic factors affect foraging behavior at bait sites. Chapter 3 is an examination of how social rank affects temporal resource partitioning at bait sites and how the resulting activity patterns influence predation risk for dominant and subordinate cohorts. Chapter 4 presents the results of a study on the spatio-temporal responses of deer to baiting and the relative harvest susceptibility of each sex-age class. Finally, Chapter 5 consists of conclusions and management implications of this research.
LITERATURE CITED


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Figure 1.1 Landcover types on 1,619 ha property in Harris County, GA (2013–2014). Mature hardwood and pine stands comprised approximately 83% (1343 ha) of the study area. Wildlife openings and row crops represented <2% of the study area.
Figure 1.2 Distribution of trough (squares) and gravity (circles) feeders during the 2013 hunting season (14 September 2013–15 January 2014) on the study area in Harris County, GA.
Figure 1.3 Distribution of trough (squares) and gravity (circles) feeders during the 2014 hunting season (13 September 2013–15 January 2014) on the study area in Harris County, GA.
CHAPTER 2

BREEDING CHRONOLOGY AND SOCIAL INTERACTIONS AFFECT UNGULATE
FORAGING BEHAVIOR AT A CONCENTRATED RESOURCE\textsuperscript{1}

\textsuperscript{1} Stone, D. B., M. J. Cherry, B. S. Cohen, J. A. Martin, and K. V. Miller. 2017. Submitted to \textit{PLOS ONE}
ABSTRACT

Prey species must balance predator avoidance behavior with other essential activities including foraging, breeding, and social interactions. Anti-predator behaviors such as vigilance can impede resource acquisition rates by altering foraging behavior. However, in addition to predation risk, vigilance levels may also be affected by socio-sexual factors including breeding chronology and social interactions. Therefore, we investigated how time-of-day, distance-to-forest, group size, social interactions (presence of different sex-age class), and breeding chronology (pre-breeding, breeding, post-breeding seasons) affected probability of feeding (hereafter: feeding) for different sex and age-classes (mature males, immature males, adult females, and juveniles) of white-tailed deer at feed sites. We developed a set of candidate models consisting of social, habitat, reproductive, and abiotic factors and combinations of these factors. We then used generalized linear mixed models (GLMMs) to estimate the probability of feeding and used model averaging of competing models for multimodel inference. Each adult sex-age class’ feeding was influenced by breeding chronology. Juveniles were more likely to be feeding than adults in all seasons. Feeding increased with group size for all sex-age classes. The presence of a mature male negatively influenced the feeding of immature males and juveniles were more likely to be feeding when an adult female was present. Feeding decreased with increasing distance-to-forest for mature males but not for other sex-age classes. Our results indicate that each sex-age class modulates vigilance levels in response to socio-sexual factors according to the unique pressures placed upon them by their reproductive status and social rank.
INTRODUCTION

Prey species must balance predator avoidance with foraging, reproductive behaviors, and social interactions (1,2). These decisions manifest in anti-predator behaviors which can hinder resource acquisition rates (1,3,4). Because predation risk varies temporally and spatially and is perceived by animals on both fine- and coarse-temporal and spatial scales (5,6), prey can modify their immediate behavioral state, social cohesion, or selection patterns to decrease predation risk. These responses include changing group size (7), selecting safer habitats (8), foraging closer to escape cover (9,10), reducing foraging activity (1), shifting foraging activity times (11), and increasing vigilance (12). Vigilance is a common metric for measuring anti-predator behavior because it is directly related to resource acquisition rates that affect prey fitness (13). However, in addition to predation risk, socio-sexual factors including sex (10), social rank (3), presence of conspecifics (14), and reproductive status (15) may also modulate vigilance behaviors.

In ungulates, sex-specific differences in vigilance are species-dependent. The demands of neonate provisioning and protection increase vigilance of females for some ungulate species, such as elk [Cervus elaphus; (10)] and moose [Alces alces; (16)]. Yet, in other ungulate species including springbok [Antidorcas marsupialis; (17)] and waterbuck [Kobus defassa; (18)], males may be more vigilant. Moreover, some ungulates, such as impala [Aepyceros melampus; (18)], show no sex-specific differences in vigilance levels. Furthermore, sex-specific vigilance depends on the animal’s reproductive status, nutritional condition, and vulnerability to predation (10,14).

When foraging in groups, an individual’s vulnerability to predation is reduced due to dilution and detection effects (19-21). However, differential sex-specific group size effects may exist in some ungulates (13,14,22). For example, Zheng et al. (2013) reported that individual vigilance decreased with increasing group size in all-female groups of Père David’s deer
(Elaphurus davidianus) but not in all-male or mixed-sex groups. In mixed-sex groups, females
did not lower their vigilance, perhaps because vigilance was not directed at predators but rather
at male conspecifics (22).

Social rank can play an important role when vigilance is directed at conspecifics (15). In
social ungulates that form aggregations governed by dominance hierarchies, subordinates direct
their vigilance at more dominant animals to avoid aggressive interactions (23). Conversely,
dominant males may show higher vigilance levels than subordinate males when defending a
harem from potential competitors (14). Agonistic interactions are energetically expensive (24)
and, when coupled with reduced resource acquisition rates while vigilant, can create a deficit in
the energy-predator avoidance balance that must be achieved for prey animals to maximize
fitness.

Ungulates exhibit variable trends in vigilance during the breeding season depending on
the breeding ecology of the species and the social rank of the individual. In harem breeders such
as elk, males are more vigilant during the breeding season than the non-breeding season (14). In
contrast, male ungulates employing a territorial breeding strategy, such as Przewalski's gazelle
[Procapra przewalskii; (15)], may invest more heavily in foraging than vigilance during the
breeding season, whereas increased vigilance by non-breeding males and females may result
from avoidance of aggression of dominant, breeding males (15).

Little is known about white-tailed deer (Odocoileus virginianus) vigilance and how social
interactions and rank, breeding chronology, and other factors affect their anti-predator behaviors.
White-tailed deer typically are sexually segregated throughout most of the year (25) with males
forming loose aggregations consisting of different age-classes outside of the breeding season
(26,27). Older and larger males tend to be dominant over immature males and adult females
Among mature males, dominance is more correlated with body mass than age (28). In contrast, dominance among females is correlated with both increasing age (28) and body mass (30). Nevertheless, large, mature males hold the highest social rank followed by adult females, immature males, and juveniles.

During the breeding season, non-estrous females may be subjected to harassment by rutting males. The duration of behavioral estrus in white-tailed deer is approximately 24 h (31) but may last >48 h (32). Consequently, during much of the breeding season, females tend to avoid rutting males. Additionally, subordinate males strive to avoid agonistic interactions with dominant males. Therefore, investigating vigilance prior to, during, and after the breeding season may offer insight on how vigilance changes in response to changes in socio-sexual factors such as breeding chronology and presence of conspecifics, in addition to perceived predation risk.

In order to better understand foraging-vigilance tradeoffs, we investigated factors influencing foraging behavior, specifically the probability of feeding at a concentrated resource. We hypothesized that each sex-age class would show unique responses to reproductive (phase of breeding season), social (presence of different sex-age class), predation risk (group size and distance-to-forest), and abiotic (time-of-day) cues. We predicted males would exhibit stronger responses to socio-sexual factors than adult females and juveniles. We predicted adult females would be most sensitive to predation risk during the pre-breeding season when their offspring were more vulnerable to predation (13,16). We predicted feeding would be greater during diurnal periods (33) but decrease as distance-to-forest increased because of greater perceived risk associated with open areas. We predicted that all sex-age classes would perceive less individual predation risk when foraging in larger groups (7,33) and consequently increase feeding. Finally, we predicted subordinate sex-age classes would decrease feeding when in the presence of a
mature male as vigilance would likely be directed at avoiding agonistic interactions with the more dominant sex-age class (13,15).

**MATERIALS AND METHODS**

_Study Area_

We conducted this study on a 1,619 ha property in Harris County, GA, USA (32.8023°N, −84.9049°W). Elevations ranged from 200 – 275m. Habitat types on the study site included a mixture of pine, pine-hardwoods, hardwood drainages, and open areas. Pine stands made up approximately 983 ha (61%) of the land cover and were comprised primarily of loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*). Hardwood stands constituted approximately 582 ha (36%) of the study site and were dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), tulip-poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*). Open areas included pasture, fallow fields, row crops, and cultivated wildlife openings. Recreational white-tailed deer hunting was allowed on the property from the second Saturday in September to 15 January. The property received minimal hunting pressure and approximately 10 (<1 deer per 160 ha) white-tailed deer were harvested annually. Non-human predators on the site included bobcats (*Lynx rufus*) and coyotes (*Canis latrans*).

_Experimental Design_

We established 22 feeding sites in a variety of habitats across the study site and used shelled corn as an attractant. Feed was presented via trough-style feeders (trough), barrel feeders (barrel), or placed directly on the ground (ground). Sites were established >2 weeks prior to data collection to allow deer to acclimate to the feeders. Once established, feed was maintained for the duration of the study.
From 13 September – 3 January in 2013 and 2014, we used infrared cameras (Reconyx Hyperfire 550, Holmen, WI, USA) to observe foraging behavior at the feed sites. We analyzed camera trap data for three days (Monday, Tuesday, and Wednesday) of each week for 16 weeks. Cameras were mounted to a tree or post 3–4 m from the feed site and approximately 75 cm from ground level. Cameras were triggered by motion and programmed to collect photographs 24hrs per day, with a 5-minute delay between successive photographs. We checked camera sites weekly to replenish bait and to replace camera batteries as needed.

We assigned each observed deer to a sex-age class [mature male (≥3.5 years-old), immature male (1.5–2.5 years-old), adult female (≥1.5 years-old), juvenile (<1.5 years-old)] based on antler and body morphology (34), and recorded the time and date of the photograph. We assigned the photograph to 1 of 3 seasons (relative to breeding season) based on conception data from the study site (35): 1) Pre-breeding -- weeks 1–6 (13 September – 25 October); 2) Breeding -- weeks 7–11 (26 October – 27 November); and 3) Post-breeding -- weeks 12–16 (28 November – 3 January). We calculated mean images per site per week for the pre-breeding, breeding, and post-breeding seasons for each sex-age class. We classified time-of-day as either diurnal (30 minutes prior to sunrise – 30 minutes after sunset) or nocturnal (>30 minutes after sunset – >30 minutes prior to sunrise) based on the median sunrise-sunset for that week. We measured the distance from the feed site to the nearest forest in all four cardinal directions using ArcMap 10.1 (36) and calculated the mean. This method more accurately characterized the openness of the habitat in which the feeding site was located than distance-to-forest in one direction only, as all feeding sites, including those that were located in open areas, were within 43m from the nearest forest edge. Distance-to-forest was standardized by calculating a z-score for the distance variable for each feeding site.
We characterized foraging behavior as “actively feeding” if the deer was consuming feed either directly from the ground or feeder. Because the method of feed presentation was not uniform across sites, we did not use head position to categorize behavioral state as done in previous studies (13,33). All other behaviors were considered “not actively feeding”. We attempted to minimize variation in behavioral interpretation by using a single observer (DBS).

We developed a set of candidate models consisting of variables known to affect foraging behavior including breeding chronology, social interactions, predation risk, and abiotic factors (Table 2.1). We then fitted generalized linear mixed models (GLMMs) to estimate the probability of feeding and treated feeding site as a random variable. We assumed a binomial distribution and used a logit link function. We first tested the residuals from the global model for serial autocorrelation in photographs for each sex-age class using the ‘acf’ function in Program R (37). All auto-correlation values were <0.1 indicating that serial auto-correlation was not an issue. We used Akaike’s Information Criteria adjusted for small sample size (AICc) and considered any model with a ΔAICc value of ≤2 as a competing model (38). We used model averaging for competing models and based our inferences on coefficients with 95% confidence intervals (CI) that did not include zero. We used the full average estimates for competing models (38).
Table 2.1 Candidate models used to predict foraging behavior of mature male (≥3.5 years-old), immature male (≤2.5 years-old), adult female (≥1.5 years-old), and juvenile (<1.5 years-old) white-tailed deer at feeding sites in Harris County, GA, USA (September-January 2013 and 2014)

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Model 1</th>
<th>Model 2</th>
<th>Model 3</th>
<th>Model 4</th>
<th>Model 5</th>
<th>Model 6</th>
<th>Model 7</th>
<th>Model 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature males</td>
<td>1) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day + Immature male*Season + Adult Female + Juvenile + Group Size</td>
<td>2) Distance-to-forest<em>Time-of-day + Immature male</em>Season + Adult Female + Juvenile + Group Size</td>
<td>3) Season<em>Time-of-day + Immature male</em>Season + Adult Female + Juvenile + Group Size</td>
<td>4) Immature male*Season + Adult Female + Juvenile + Group Size</td>
<td>5) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day</td>
<td>6) Season*Time-of-day</td>
<td>7) Distance-to-forest*Time-of-day</td>
<td>8) Null</td>
</tr>
<tr>
<td>Immature males</td>
<td>1) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day + Mature male*Season + Adult Female + Juvenile + Group Size</td>
<td>2) Distance-to-forest<em>Time-of-day + Mature male</em>Season + Adult Female + Juvenile + Group Size</td>
<td>3) Season<em>Time-of-day + Mature male</em>Season + Adult Female + Juvenile + Group Size</td>
<td>4) Mature male*Season + Adult Female + Juvenile + Group Size</td>
<td>5) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day</td>
<td>6) Season*Time-of-day</td>
<td>7) Distance-to-forest*Time-of-day</td>
<td>8) Null</td>
</tr>
<tr>
<td>Adult females</td>
<td>1) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day + Mature male + Immature Male + Juvenile*Season + Group Size</td>
<td>2) Distance-to-forest<em>Time-of-day + Mature male + Immature Male + Juvenile</em>Season + Group Size</td>
<td>3) Season<em>Time-of-day + Mature male + Immature Male + Juvenile</em>Season + Group Size</td>
<td>4) Mature male*Season + Adult Female + Juvenile + Group Size</td>
<td>5) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day</td>
<td>6) Season*Time-of-day</td>
<td>7) Distance-to-forest*Time-of-day</td>
<td>8) Null</td>
</tr>
<tr>
<td>Juveniles</td>
<td>1) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day + Mature male+ Immature Male + Adult Female*Season + Group Size</td>
<td>2) Distance-to-forest<em>Time-of-day + Mature male + Immature Male + Adult Female</em>Season + Group Size</td>
<td>3) Season<em>Time-of-day + Mature male+ Immature Male + Adult Female</em>Season + Group Size</td>
<td>4) Mature male<em>Season + Adult Female + Adult Female</em>Season + Group Size</td>
<td>5) Distance-to-forest<em>Time-of-day + Season</em>Time-of-day</td>
<td>6) Season*Time-of-day</td>
<td>7) Distance-to-forest*Time-of-day</td>
<td>8) Null</td>
</tr>
</tbody>
</table>

Predictor variables include standardized distance-to-forest, time-of-day (day=1, night=0), season (pre-breeding, breeding, post-breeding), presence of a mature male, presence of an immature male, presence of an adult female, presence of a juvenile, group size, year, feeder type, and feeding site. Each model included year, feeder type, and feeding site. Feeding site was treated as a random effect.
We included the interactions between distance-to-forest and time-of-day as well as distance-to-forest and season. For the mature and immature male models, we included an interaction between their presence and season. Additionally, for the adult female and juvenile models, we included interaction terms for their presence in the respective models and season. To control for potential differences in feeding rates influenced by year and feeder type, we included year and feeder type in each of our candidate models. We used Program R 3.1.2 for all statistical analyses (37).

RESULTS

Camera trapping effort was 375, 411, and 402 camera days for the pre-breeding, breeding, and post-breeding seasons, respectively. We collected 6,994 photographs containing images of 8,469 white-tailed deer for which we could assign a sex-age class. We recorded a total of 2,078 mature male, 2,479 immature male, 2,225 adult female, and 1,687 juvenile images.

Mean photos per site per week (hereafter: photographic occurrences; \( \bar{x} \pm se \)) were greatest during the post-breeding season for mature males (8.23 ± 0.89), immature males (11.39 ± 1.01), and juveniles (6.63 ± 0.65). Mean photographic occurrences were fewest during the breeding season for mature males (2.53 ± 0.37) and immature males (2.38 ± 0.32). In contrast, adult female photographic occurrences were similar among the pre-breeding (7.81 ± 1.38), breeding (5.71 ± 0.74), and post-breeding (6.78 ± 0.59) seasons.

Because of very few (\( n = 6 \)) observations of mature males and adult females occurring in the same photograph, we failed to obtain convergence for the adult female and mature male models when we included their presence in the respective models. We also failed to obtain convergence for the mature male and immature male models when we included the seasonal interaction. Therefore, we removed those variables from the respective models.
Mature male feeding was best explained by model 1 that included distance-to-forest \( x \) time-of-day interaction, season \( x \) time-of-day interaction, presence of an immature male, presence of an adult female, presence of a juvenile, group size, year, feeder type, and feeding site (Table 2.2). Neither the distance-to-forest \( x \) time-of-day interaction nor the season \( x \) time-of-day interaction was significant. Feeding increased with increasing group size, decreased with increasing distance-to-forest, and was greatest during the breeding season (Table 2.3, Figure 2.1).

**Table 2.2** Model selection results for models used to predict the probability of foraging for mature male (≥3.5 years-old), immature male (≤2.5 years-old), adult female (≥1.5 years-old), and juvenile (<1.5 years-old) white-tailed deer at feeding sites in Harris County, GA, USA (September-January 2013 and 2014). Models presented received the most support of our candidate models (\( \Delta \text{AICc} < 2 \)).

<table>
<thead>
<tr>
<th>Sex-age Class</th>
<th>Model(^a)</th>
<th>K</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>Weight</th>
<th>Log-likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature Male</td>
<td>1) D<em>T + S</em>T + IM + AF + J + GS</td>
<td>15</td>
<td>1672.64</td>
<td>0.00</td>
<td>1.0</td>
<td>-821.20</td>
</tr>
<tr>
<td>Immature Male</td>
<td>1) D<em>T + S</em>T + MM + AF + J + GS</td>
<td>16</td>
<td>2104.97</td>
<td>0.00</td>
<td>0.47</td>
<td>-1036.38</td>
</tr>
<tr>
<td></td>
<td>3) S*T + MM + AF + J + GS</td>
<td>14</td>
<td>2106.33</td>
<td>1.35</td>
<td>0.24</td>
<td>-1039.08</td>
</tr>
<tr>
<td>Adult Female</td>
<td>1) D<em>T + S</em>T + IM + J*S + GS</td>
<td>17</td>
<td>2233.03</td>
<td>0.00</td>
<td>0.36</td>
<td>-1099.37</td>
</tr>
<tr>
<td></td>
<td>3) S<em>T + IM + J</em>S + GS</td>
<td>15</td>
<td>2233.22</td>
<td>0.19</td>
<td>0.33</td>
<td>-1101.50</td>
</tr>
<tr>
<td></td>
<td>4) IM + J*S + GS</td>
<td>12</td>
<td>2234.04</td>
<td>1.02</td>
<td>0.22</td>
<td>-1104.95</td>
</tr>
<tr>
<td>Juvenile</td>
<td>4) IM + AF*S + GS</td>
<td>12</td>
<td>1905.68</td>
<td>0.00</td>
<td>0.77</td>
<td>-940.75</td>
</tr>
</tbody>
</table>

\(^a\)Predictor variables include standardized distance-to-forest (D), time-of-day (T), season (S), presence of a mature male (MM), presence of an immature male (IM), presence of an adult female (AF), presence of a juvenile (J), and group size (GS). Year, feeder type, and feeding site were included in all models. Feeding site was treated as a random effect.
Figure 2.1 Probability of foraging for mature males (≥3.5 years-old), immature males (≤2.5 years-old), adult females (≥1.5 years-old), and juveniles (≤1.5 years-old) during the pre-breeding (13 September – 25 October), breeding (26 October – 27 November), and post-breeding (28 November – 3 January) seasons of 2013 – 2014 in Harris County, GA, USA. Error bars represent ±1 standard error.
Table 2.3 Parameter estimates for generalized linear mixed model predicting the probability of foraging for mature male (≥3.5 years-old) white-tailed deer in Harris County, GA, USA, September–January, 2013–2014

<table>
<thead>
<tr>
<th>Term</th>
<th>β</th>
<th>SE</th>
<th>z value</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.00</td>
<td>0.38</td>
<td>-5.25</td>
<td>-2.752</td>
<td>-1.256</td>
</tr>
<tr>
<td>Post-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.49</td>
<td>0.21</td>
<td>-2.32</td>
<td>-0.908</td>
<td>-0.076</td>
</tr>
<tr>
<td>Pre-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.71</td>
<td>0.23</td>
<td>-3.11</td>
<td>-1.157</td>
<td>-0.261</td>
</tr>
<tr>
<td>IM&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-0.29</td>
<td>0.33</td>
<td>-0.89</td>
<td>-0.930</td>
<td>0.348</td>
</tr>
<tr>
<td>J&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-0.56</td>
<td>0.57</td>
<td>-0.97</td>
<td>-1.678</td>
<td>0.566</td>
</tr>
<tr>
<td>Y&lt;sup&gt;f&lt;/sup&gt;</td>
<td>-1.18</td>
<td>0.20</td>
<td>-5.94</td>
<td>-1.568</td>
<td>-0.790</td>
</tr>
<tr>
<td>GS&lt;sup&gt;g&lt;/sup&gt;</td>
<td>1.06</td>
<td>0.23</td>
<td>4.62</td>
<td>0.610</td>
<td>1.509</td>
</tr>
<tr>
<td>FT&lt;sup&gt;hi&lt;/sup&gt;</td>
<td>0.57</td>
<td>0.42</td>
<td>1.37</td>
<td>-0.245</td>
<td>1.387</td>
</tr>
<tr>
<td>FT&lt;sup&gt;hj&lt;/sup&gt;</td>
<td>-0.28</td>
<td>0.35</td>
<td>-0.80</td>
<td>-0.961</td>
<td>0.405</td>
</tr>
<tr>
<td>D x T</td>
<td>0.24</td>
<td>0.20</td>
<td>1.19</td>
<td>-0.156</td>
<td>0.643</td>
</tr>
<tr>
<td>T x Post-breeding</td>
<td>0.11</td>
<td>0.38</td>
<td>0.29</td>
<td>-0.628</td>
<td>0.844</td>
</tr>
<tr>
<td>T x Pre-breeding</td>
<td>-0.21</td>
<td>0.52</td>
<td>-0.40</td>
<td>-1.231</td>
<td>0.810</td>
</tr>
</tbody>
</table>

<sup>*</sup> Indicates 95% confidence interval does not include zero.

<sup>a</sup> Standardized distance-to-forest
<sup>b</sup> Time-of-day (1=diurnal, 0=nocturnal)
<sup>c</sup> Compared to reference class: breeding season
<sup>d</sup> Presence of an immature male
<sup>e</sup> Presence of a juvenile
<sup>f</sup> Year
<sup>g</sup> Group size
<sup>h</sup> Feeder type, compared to reference class: barrel feeder
<sup>i</sup> Feeder type = ground
<sup>j</sup> Feeder type = trough
Immature male feeding was best explained by models 1 and 3 (Table 2.2). The top models included distance-to-forest x time-of-day interaction, season x time-of-day interaction, presence of a mature male, presence of an adult female, presence of a juvenile, group size, year, feeder type, and feeding site. Neither the distance-to-forest x time-of-day interaction nor the season x time-of-day interaction was significant. Feeding increased with increasing group size, decreased when a mature male was present, and was greater during the pre-breeding and breeding seasons than the post-breeding season (Table 2.4, Figure 2.1).
Table 2.4 Parameter estimates for generalized linear mixed model predicting the probability of foraging for immature male (≤2.5 years-old) white-tailed deer in Harris County, GA, USA, September–January, 2013–2014

<table>
<thead>
<tr>
<th></th>
<th>β</th>
<th>SE</th>
<th>z value</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.04</td>
<td>0.29</td>
<td>6.95</td>
<td>-2.621</td>
<td>-1.469</td>
</tr>
<tr>
<td>D&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-0.01</td>
<td>0.09</td>
<td>0.09</td>
<td>-0.193</td>
<td>0.176</td>
</tr>
<tr>
<td>T&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.01</td>
<td>0.35</td>
<td>0.03</td>
<td>-0.668</td>
<td>0.687</td>
</tr>
<tr>
<td>Post-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.45</td>
<td>0.20</td>
<td>2.24</td>
<td>-0.850</td>
<td>-0.058</td>
</tr>
<tr>
<td>Pre-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.04</td>
<td>0.22</td>
<td>0.18</td>
<td>-0.384</td>
<td>0.460</td>
</tr>
<tr>
<td>MM&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-0.88</td>
<td>0.32</td>
<td>2.70</td>
<td>-1.510</td>
<td>-0.241</td>
</tr>
<tr>
<td>AF&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-0.25</td>
<td>0.55</td>
<td>0.46</td>
<td>-1.336</td>
<td>0.833</td>
</tr>
<tr>
<td>J&lt;sup&gt;f&lt;/sup&gt;</td>
<td>-0.25</td>
<td>0.43</td>
<td>0.57</td>
<td>-1.094</td>
<td>0.603</td>
</tr>
<tr>
<td>Y&lt;sup&gt;g&lt;/sup&gt;</td>
<td>0.01</td>
<td>0.15</td>
<td>0.06</td>
<td>-0.280</td>
<td>0.299</td>
</tr>
<tr>
<td>GS&lt;sup&gt;h&lt;/sup&gt;</td>
<td>0.45</td>
<td>0.17</td>
<td>2.70</td>
<td>0.124</td>
<td>0.783</td>
</tr>
<tr>
<td>FT&lt;sup&gt;i&lt;/sup&gt;&lt;sub&gt;j&lt;/sub&gt;</td>
<td>0.56</td>
<td>0.25</td>
<td>2.20</td>
<td>0.062</td>
<td>1.059</td>
</tr>
<tr>
<td>FT&lt;sup&gt;i&lt;/sup&gt;&lt;sub&gt;k&lt;/sub&gt;</td>
<td>-0.19</td>
<td>0.21</td>
<td>0.90</td>
<td>-0.599</td>
<td>0.223</td>
</tr>
<tr>
<td>D x T</td>
<td>-0.23</td>
<td>0.21</td>
<td>1.09</td>
<td>-0.636</td>
<td>0.181</td>
</tr>
<tr>
<td>T x Post-breeding&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0.34</td>
<td>0.38</td>
<td>0.88</td>
<td>-0.413</td>
<td>1.088</td>
</tr>
<tr>
<td>T x Pre-breeding&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-0.11</td>
<td>0.43</td>
<td>0.25</td>
<td>-0.956</td>
<td>0.739</td>
</tr>
</tbody>
</table>

* Indicates 95% confidence interval does not include zero

<sup>a</sup> Standardized distance-to-forest
<sup>b</sup> Time-of-day (1=diurnal, 0=nocturnal)
<sup>c</sup> Compared to reference class: breeding season
<sup>d</sup> Presence of a mature male
<sup>e</sup> Presence of an adult female
<sup>f</sup> Presence of a juvenile
<sup>g</sup> Year
<sup>h</sup> Group Size
<sup>i</sup> Feeder type, compared to reference class: barrel feeder
<sup>j</sup> Feeder type = ground
<sup>k</sup> Feeder type = trough
Adult female feeding was best explained by models 1, 3, and 4 (Table 2.2). The top models included distance-to-forest \times time-of-day interaction, season \times time-of-day interaction, presence of an immature male, presence of a juvenile \times season interaction, group size, year, feeder type, and feeding site. None of the interactions were significant. Feeding increased with increasing group size and was greatest during the post-breeding season (Table 2.5, Figure 2.1).

Juvenile feeding was best explained by model 4 (Table 2.2). The top model included presence of an immature male, presence of an adult female \times season interaction, group size, year, feeder type, and feeding site. The presence of an adult female \times season interaction was not significant. Feeding increased with increasing group size and when an adult female was present (Table 2.6). Juvenile feeding was not influenced by breeding chronology (Table 2.6, Figure 2.1).
**Table 2.5** Parameter estimates for generalized linear mixed model predicting the probability of foraging for adult female (≥1.5 years-old) white-tailed deer in Harris County, GA, USA, September–January, 2013–2014

<table>
<thead>
<tr>
<th></th>
<th>( \beta )</th>
<th>SE</th>
<th>z value</th>
<th>Lower CI</th>
<th>Upper CI</th>
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</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.46</td>
<td>0.27</td>
<td>8.94</td>
<td>-2.994</td>
<td>-1.918</td>
</tr>
<tr>
<td>( D^a )</td>
<td>-0.11</td>
<td>0.16</td>
<td>0.69</td>
<td>-0.425</td>
<td>0.204</td>
</tr>
<tr>
<td>( T^b )</td>
<td>0.40</td>
<td>0.30</td>
<td>1.33</td>
<td>-0.189</td>
<td>0.991</td>
</tr>
<tr>
<td>Post-breeding(^c)</td>
<td>0.48</td>
<td>0.22</td>
<td>2.18</td>
<td>0.048</td>
<td>0.918</td>
</tr>
<tr>
<td>Pre-breeding(^c)</td>
<td>0.40</td>
<td>0.21</td>
<td>1.89</td>
<td>-0.015</td>
<td>0.812</td>
</tr>
<tr>
<td>( IM^d )</td>
<td>0.01</td>
<td>0.44</td>
<td>0.03</td>
<td>-0.847</td>
<td>0.876</td>
</tr>
<tr>
<td>( J^e )</td>
<td>0.28</td>
<td>0.24</td>
<td>1.18</td>
<td>-0.187</td>
<td>0.752</td>
</tr>
<tr>
<td>( Y^f )</td>
<td>-0.17</td>
<td>0.19</td>
<td>0.91</td>
<td>-0.544</td>
<td>0.200</td>
</tr>
<tr>
<td>( GS^g )</td>
<td>0.24</td>
<td>0.08</td>
<td>2.87</td>
<td>0.076</td>
<td>0.402</td>
</tr>
<tr>
<td>( FT^hi )</td>
<td>0.88</td>
<td>0.33</td>
<td>2.64</td>
<td>0.226</td>
<td>1.535</td>
</tr>
<tr>
<td>( FT^hj )</td>
<td>0.45</td>
<td>0.29</td>
<td>1.54</td>
<td>-0.124</td>
<td>1.030</td>
</tr>
<tr>
<td>( D \times T )</td>
<td>0.04</td>
<td>0.10</td>
<td>0.40</td>
<td>-0.155</td>
<td>0.235</td>
</tr>
<tr>
<td>( T \times Post-breeding )</td>
<td>-0.61</td>
<td>0.43</td>
<td>1.41</td>
<td>-1.456</td>
<td>0.239</td>
</tr>
<tr>
<td>( T \times Pre-breeding )</td>
<td>-0.40</td>
<td>0.34</td>
<td>1.18</td>
<td>-1.074</td>
<td>0.265</td>
</tr>
<tr>
<td>( J \times Post-breeding )</td>
<td>-0.52</td>
<td>0.29</td>
<td>1.78</td>
<td>-1.082</td>
<td>0.051</td>
</tr>
<tr>
<td>( J \times Pre-breeding )</td>
<td>-0.19</td>
<td>0.29</td>
<td>0.64</td>
<td>-0.754</td>
<td>0.382</td>
</tr>
</tbody>
</table>

\(^a\) Indicates 95% confidence interval does not include zero

\(^a\) Standardized distance-to-forest

\(^b\) Time-of-day (1=diurnal, 0=nocturnal)

\(^c\) Compared to reference class: breeding season

\(^d\) Presence of an immature male

\(^e\) Presence of a juvenile

\(^f\) Year

\(^g\) Group Size

\(^h\) Feeder type, compared to reference class: barrel feeder

\(^i\) Feeder type = ground

\(^j\) Feeder type = trough
Table 2.6 Parameter estimates for generalized linear mixed model predicting the probability of foraging for juvenile (<1.5 years-old) white-tailed deer in Harris County, GA, USA, September–January, 2013–2014

<table>
<thead>
<tr>
<th></th>
<th>β</th>
<th>SE</th>
<th>z value</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.58</td>
<td>0.25</td>
<td>-6.24</td>
<td>-2.075</td>
<td>-1.083</td>
</tr>
<tr>
<td>Post-breeding&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-0.34</td>
<td>0.20</td>
<td>1.70</td>
<td>-0.730</td>
<td>0.053</td>
</tr>
<tr>
<td>Pre-breeding&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.04</td>
<td>0.25</td>
<td>0.15</td>
<td>-0.444</td>
<td>0.518</td>
</tr>
<tr>
<td>MM&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-0.02</td>
<td>0.50</td>
<td>-0.05</td>
<td>-1.007</td>
<td>0.959</td>
</tr>
<tr>
<td>IM&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.13</td>
<td>0.36</td>
<td>0.37</td>
<td>-0.572</td>
<td>0.834</td>
</tr>
<tr>
<td>AF&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.66</td>
<td>0.29</td>
<td>2.27</td>
<td>0.090</td>
<td>1.221</td>
</tr>
<tr>
<td>Y&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-0.56</td>
<td>0.18</td>
<td>-3.12</td>
<td>-0.914</td>
<td>-0.209</td>
</tr>
<tr>
<td>GS&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.26</td>
<td>0.13</td>
<td>2.02</td>
<td>0.008</td>
<td>0.520</td>
</tr>
<tr>
<td>FT&lt;sup&gt;gh&lt;/sup&gt;</td>
<td>0.92</td>
<td>0.25</td>
<td>3.63</td>
<td>0.423</td>
<td>1.420</td>
</tr>
<tr>
<td>FT&lt;sup&gt;gi&lt;/sup&gt;</td>
<td>0.39</td>
<td>0.18</td>
<td>2.14</td>
<td>0.032</td>
<td>0.756</td>
</tr>
<tr>
<td>AF*Post-breeding</td>
<td>-0.04</td>
<td>0.28</td>
<td>-0.15</td>
<td>-0.600</td>
<td>0.514</td>
</tr>
<tr>
<td>AF*Pre-breeding</td>
<td>-0.35</td>
<td>0.32</td>
<td>-1.11</td>
<td>-0.979</td>
<td>0.273</td>
</tr>
</tbody>
</table>

* Indicates confidence interval does not include zero
<sup>a</sup> Compared to reference class: breeding season
<sup>b</sup> Presence of a mature male
<sup>c</sup> Presence of an immature male
<sup>d</sup> Presence of an adult female
<sup>e</sup> Year
<sup>f</sup> Group Size
<sup>g</sup> Feeder type, compared to reference class: barrel feeder
<sup>h</sup> Feeder type = ground
<sup>i</sup> Feeder type = trough
DISCUSSION

Our results demonstrate that sex-age class-specific foraging behavior is the result of complex relationships among reproductive chronology, social factors, and predation risk. Individually, these factors have been shown to affect anti-predator behaviors for a wide variety of species, but evidence of how they interact to produce sex-age class-specific vigilance is lacking. In the present study, deer appeared to alter foraging behavior in response to socio-sexual factors within the constraints of background predation risk.

While feeding was similar for all adult sex-age classes during the breeding season, each responded differently to breeding chronology. A breeding male’s strategy for meeting energy-maximizing and time-minimizing requirements (39) during the breeding season may be more effective when utilizing a consistent, high-energy food resource at a feeding site. As with many ungulate species, male white-tailed deer exhibit hypophagia during the breeding season (40,41) and focus time investments in mate searching rather than foraging. Similar to Ozoga and Verme (1982) we noted that adult males visited feeders at lower rates than females and fawns during the breeding season. However, they apparently optimized forage acquisition at these sites by spending a greater proportion of time actively feeding.

During the breeding season, male group size decreases, presumably leading to increased individual predation risk. Our results indicated that mean group size was lowest during the breeding season (1.06 ± 0.01). Additionally, the risk of agonistic encounters with rival males imposes greater social risk during this time. Despite an increase in predation and social risk during the breeding season, mature male feeding did not reflect the change in risk.

Immature male feeding did not differ from the pre-breeding to breeding season but was reduced during the post-breeding season. Decreased feeding by immature males during the post-
breeding season may have resulted from conspecific-directed vigilance (14,22). Competition and social rank have been used to explain alterations of vigilance levels in ungulates including impala (42), elk (14), Przewalski’s gazelle (15), and Père David’s deer (22). Although we could not obtain convergence for our immature male model when including a season and mature male interaction, we observed 1.9x as many photographs per week of mature males and immature males together during post-breeding season than during the pre-breeding season. Consequently, immature males may have increased vigilance toward mature males during the post-breeding season.

Juveniles were more likely to be feeding than adults during all seasons. Juveniles are generally less wary than adults despite typically being the most vulnerable demographic. Also, because juveniles typically do not reach sexual maturity during their first year in the southeastern U.S., their activity budget focuses more on body growth (13) than reproduction. We detected an increase in juvenile feeding when adult females were present but, interestingly, adult female feeding was not affected by the presence of a juvenile.

We predicted that adult females would feed least during the pre-breeding season when their fawns were more susceptible to predation as the survival of their offspring determines their lifetime fitness (43). However, our results did not support this prediction. According to Williams (1966), a parent should maximize lifetime fitness by balancing investment in present and future reproduction. In our study, juveniles were likely weaned by the beginning of data collection. Because dams should base their investment decisions on the value of their current offspring relative to future reproduction (44), adult females may invest more heavily in future reproduction via their own survival (i.e. not increasing vigilance at the cost of decreasing their own fitness through reduced resource acquisition rates) than in the survival of the juvenile. Cherry et al.
(2015) suggested that there is a point at which females must allocate more energy to personal nutrition to foster gestation than to protection of their offspring.

Distance to escape cover is an important consideration for animals when making foraging decisions (9,45). Animals perceive predation risk at multiple spatial scales and alter anti-predator behavior in response to the perceived predation risk associated with specific locations (10). Lagory (1989) found that white-tailed deer vigilance decreased in more open areas. However, Lagory (1986) investigated this relationship on an island where predators had been extirpated for many years. To the contrary, we hypothesized that feeding would decrease with increasing distance-to-forest because, in general, cover benefits prey with cursorial predators. We found that feeding decreased with increasing distance-to-forest for mature males only.

Each sex-age class increased feeding with increasing group size. Previous studies on white-tailed deer vigilance demonstrated that males and females decreased vigilance when foraging in larger groups (7,27,33). Cherry et al. (2015), however, reported an increase in proportion of time spent feeding with increasing group size for females and juveniles but not males. They attributed the lack of response by males to increasing group size to intra-specific competition at a concentrated resource and timing of sampling relative to breeding chronology. Our research investigated group size-feeding relationships at a broad temporal scale (September – January) and, therefore, may not have detected finer temporal scale responses by males.

How prey animals alter vigilance in response to changes in breeding chronology, social dynamics, environmental, and habitat-related factors is important for understanding underlying drivers of ecological processes. Behavioral modifications induced by predation risk can have cascading effects on plant and animal communities (46,47), especially in systems characterized by abundant herbivore populations. In addition to balancing the tradeoffs between resource
acquisition and predator avoidance, animals must also alter behavior in accordance with the cost-benefits of vigilance directed at conspecifics (14). Our results suggest that within a single species, each sex-age class shows differential responses to socio-sexual factors within the constraints of predation risk. Given the recent changes in the distribution and abundance of non-human predators to landscapes that many prey populations inhabit (48-50), future research comparing the relative influences of socio-sexual and predation risk on vigilance behaviors are warranted.

ACKNOWLEDGEMENTS:

We would like to thank land owners for access to their properties and D. Crawford and C. Evans for assistance with field data collection. Funding for this project was provided by the Georgia Wildlife Resources Division through the Wildlife Restoration Program, which derives monies through an excise tax on sporting arms and ammunition paid by hunters and recreational shooters.
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CHAPTER 3

INTRASPECIFIC TEMPORAL RESOURCE PARTITIONING AT UNGULATE FEEDING SITES: IMPLICATIONS FOR DIFFERENTIAL PREDATION RISK

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ABSTRACT

Individuals may reduce competition by temporally partitioning their use of a shared resource. The social factors hypothesis suggests that behavioral differences between sexes in ungulates encourage segregation as individuals attempt to avoid antagonistic interactions. However, dominant cohorts may reduce subordinates’ access to food resources, regardless of sex. We hypothesized that white-tailed deer (*Odocoileus virginianus*) temporally segregated at supplemental feeding sites based on social rank and that segregation was affected by phase of the breeding season (pre-breed, breed, and post-breed) and diel cycle (diurnal or nocturnal hours). If cohorts are temporally segregating, we predicted that the resulting activity patterns would manifest in one cohort being relatively more susceptible to hunter-induce mortality. To quantify temporal segregation at feeding sites, we used multi-state modeling to determine the probabilities for feeding sites (*n* = 16) to transition from 1 of 4 states (1-no deer present, 2-subordinate cohort present, 3-dominant cohort present, 4-both subordinate and dominant cohort present) to a different state. Additionally, we calculated the probability that a feeding site was in a particular state during diurnal and nocturnal hours during the 3 phases of the breeding season. We determined that transition probabilities differed by season and diel cycle and dominant and subordinate cohorts clearly avoided each other at the feeding sites.

INTRODUCTION

Individuals may reduce competition by partitioning resources temporally and spatially (Schoener 1971; Ziv et al. 1993, Howerton and Mench 2014). Temporal resource partitioning, in particular, can be vital to the coexistence of species, or individuals, that share a common resource (Ziv et al. 1993). Mechanisms driving temporal resource partitioning are similar for inter- and intra-specific
competition. The Social Factors Hypothesis (Bowyer 2004) suggests that sex-specific behavioral differences in ungulate resource use increases segregation as individuals attempt to avoid antagonistic interactions. However, interference competition from dominant cohorts may reduce subordinates’ access to food resources, regardless of sex (Appleby 1980; Schmidt and Seivwright 1997, Schmidt et al. 1998, Putman and Staines 2004, McGhee and Baccus 2006, Donohue et al. 2013). For example, subordinate male red deer (*Cervus elaphus*) may avoid using feeding sites when patch profitability does not outweigh the costs of agonistic interactions with dominant males (Schmidt et al. 1998). Additionally, Grenier et al. (1999) reported that female and fawn white-tailed deer had greater access to food when adult males were not present.

Older, larger ungulate males are generally dominant over smaller males and females (Ozoga 1972, Townsend and Bailey 1981, Appleby 1982, Grenier et al. 1999, Côté 2000, Donohue et al. 2013), but dominance hierarchies are seasonally dynamic (Koutnik 1981, Grovenburg et al. 2009). *Odocoileus* spp. exhibit marked sexual segregation outside of the breeding season with males forming loose aggregations that consist of various age classes (Hirth 1977, Lagory 1986, Miller and Conner 2005). Female groups consist of a matriarchal female, multiple generations of her female offspring, and pre-dispersal males (Hirth 1977, Lagory 1986). Male dispersal typically occurs in their first spring or second autumn (Rosenberry et al. 1999). Therefore, during autumn, yearling males may be solitary or associate with either matrilineal or all-male groups. Regardless of their social affiliation, yearling males are competitively disadvantaged compared to adult males (Donohue et al. 2013).

Competitive asymmetries are common at concentrated resources (Ozoga and Verme 1982, Pimm et al. 1985, Donohue et al. 2013). It is possible that in populations with clear dominance hierarchies, competition drives temporal resource partitioning. Furthermore, if
competitors temporally segregate use of a shared resource, subordinates may use the resource only when dominant cohorts are absent. Resulting activity patterns at the resource may enhance or diminish susceptibility to predation, depending on the suite of predators and their associated activity cycle.

Temporal resource partitioning has been studied in sympatric species of mammals (Kronfeld-Schor and Dayan 1999, Jacamo et al. 2004, Adams and Thibault 2006). However, the effect of social rank on intraspecific temporal resource partitioning has not been investigated in ungulates. We hypothesized that white-tailed deer would temporally segregate use of supplemental feed sites based on competitive status whereby adult females and yearling males would avoid encounters with adult males. Moreover, if we observed temporal resource partitioning based on competitive status, we hypothesized that activity patterns at the feeding sites would manifest in one cohort being more at risk to hunter-induced mortality. We tested these hypotheses in a population of white-tailed deer offered supplemental feed during the hunting season.

MATERIALS AND METHODS

Study area—We conducted this study on a 1,619-ha property in Harris County, GA, USA (32.8023°N, −84.9049°W). Pine stands made up approximately 983 ha (61%) of the land cover and were comprised primarily of loblolly (Pinus taeda) and shortleaf pine (P. echinata). Hardwood stands constituted approximately 582 ha (36%) of the study site and were dominated by oak (Quercus spp.), hickory (Carya spp.), tulip-poplar (Liriodendron tulipifera), and sweetgum (Liquidambar styraciflua). Open areas included pasture, fallow fields, row crops, and cultivated wildlife openings. White-tailed deer hunting occurred on the property from the second Saturday in September to 15 January. The property received light hunting pressure and
approximately 10 deer (<1 deer per 160 ha) were harvested annually. Hunter effort data indicated that on average, one hunt (i.e., a single hunter from a fixed location) occurred every 2 days.

Non-human predators on the site included bobcats (Lynx rufus) and coyotes (Canis latrans). Although coyotes can affect fawn survival in some regions (Ballard 2011), they are not effective predators of adult deer in the southeastern United States (Chitwood et al. 2014). Where bobcats are sympatric with coyotes, food habit studies indicate that bobcats are not responsible for significant direct mortality on adult deer (VanGilder 2008).

Experimental Design—We established 16 feeding sites across the study site and used shelled corn as supplemental forage. We provided feed ad libitum throughout the duration of the study, which began >2 weeks prior to data collection to allow deer to acclimate to the feeding sites. From 13 September – 3 January in 2013 and 2014, we used infrared cameras (Reconyx Hyperfire 550, Holmen, WI, USA) to observe visitation rates. We mounted cameras to a tree or post 3 – 4 m from the feed site and approximately 75 cm from ground level. Cameras recorded photographs 24 hrs per day, with a 5-minute delay between successive photographs. We assigned each deer observation to a sex-age class [adult male (≥2.5 years-old), yearling male (1.5 years-old), and adult female (≥1.5 years-old)] based on antler and body morphology (Richards and Brothers 2003), and recorded the time and date of the photograph. Adult male dominance at concentrated resources is well documented in white-tailed deer (Ozoga 1972, Weeks 1978, Donohue et al. 2013). Because both yearling males and adult females are subordinate to adult males during autumn, we pooled their observations. We excluded photographs when the sex-age class for all individuals in the photograph could not be determined.

Although adult males are dominant throughout autumn and early winter, social dynamics and the frequency of aggressive interactions change relative to the breeding season (Hirth 1977).
Furthermore, physiological and behavioral changes related to breeding activity occur in males and could affect the degree of temporal partitioning. Therefore, we divided the study period into pre-breeding, breeding, and post-breeding seasons based on conception data from the study site (Stickles et al. 2015): 1) Pre-breeding -- weeks 1–6 (13 September – 25 October); 2) Breeding -- weeks 7–11 (26 October – 27 November); and 3) Post-breeding -- weeks 12–16 (28 November – 3 January).

We analyzed camera data for three days (Monday, Tuesday, and Wednesday) of each week. We binned each observation of a deer at a feeding site by hour of the day (0-23). We divided the diel cycle into diurnal and nocturnal hours based on legal hunting hours to determine the relative exposure of each cohort to human predators. We used the hours in which legal hunting began and ended for our delineation of diurnal and nocturnal hours.

*Models*—We used multi-state modeling in package ‘msm’ (Jackson 2011) for R version 3.1.2 (R Core Team 2014) to calculate the probability of a feeding site being in one of four possible states. In any given hour, the feeding site could have been in State 1 (no deer present), State 2 (subordinate present), State 3 (dominant present), or State 4 (both a dominant and subordinate present concurrently). We used all photographs recorded during each hour to determine the state of the feeder. For example, if all of the photographs collected during a given hour at a particular feeding site were of adult males and we collected no photos of adult females or yearling males during that hour, the state of the feeding site for that hour was State 3 (dominant present). Likewise, if an adult female and an adult male were photographed during a given hour at a particular feeding site, the state of the feeding site for that hour was State 4 (both a subordinate and a dominant present). To determine if deer temporally segregated use of the feeding site based on social rank, we first quantified the temporal segregation between dominants
and subordinates (Segregation Model; hereafter: SM). We used multi-state Markov modeling to calculate the hazard ratios (HRs) and transition probabilities (TPs). Because feeding sites were available to all deer during all hours, we considered all transitions equally possible. Therefore, we assigned each transition a value of 0.25 in the transition intensity matrix. We estimated hazard ratios and transition probabilities by season (pre-breed, breed, and post-breed) and time-of-day (diurnal or nocturnal), and used ‘state’ as the response variable in our model. Hazard ratio values of 1 indicate that the transition probabilities did not differ according to season or time-of-day (Jackson 2011; see Figure 3.1 for transition diagram).

Additionally, we estimated probabilities of a feeding site going from one state at time \( t \) to a different state at time \( t+1 \) during each season and period. Transition probabilities from State 1 to any other state are not dependent on the presence of other cohorts at a feeding site; therefore these values are expected to be equal (see Prediction 1, Table 3.1). Furthermore, if the presence of either cohort at time \( t \) does not affect the probability of another cohort being present at time \( t+1 \), we expect the transition probability from one cohort to another to be equal to the probability of transitioning to a no deer state (see Prediction 2, Table 3.1).

To determine if dominants and subordinates are temporally segregating at the feeding sites, we investigated if partitioning manifested in differential arrival times and use. Therefore, we implemented Markov chain Monte Carlo (MCMC) routines to fit a multinomial response (States 1–4) generalized linear mixed models in package ‘MCMCglmm’ (Hadfield 2010) (Diel Model; hereafter DM). We modeled the response (state) by season, diel phase (diurnal or nocturnal hours), and their interactions. We treated the feeding site as a random effect.
RESULTS

Hazard ratios from the segregation model indicated that transition probabilities (TPs) varied according to season and the diel cycle. During the pre-breeding season, transitions 1–2 (HR, 95% confidence interval; HR = 1.61, CI = 1.25–2.08) and 1–3 (HR = 1.77, CI = 1.39–2.25) were more likely to occur than during the breeding season (Table 3.2). Transition 3–1 was less likely to occur in the pre-breeding (HR = 0.78, CI= 0.61–0.98) and post-breeding (HR = 0.75, CI = 0.60–0.94) seasons than in the breeding season (Tables 3.2 and 3.3). Compared to the breeding season, TPs for transitions 1–2 (HR = 2.91, CI = 2.28–3.71), 1–3 (HR = 2.93, CI = 2.32–3.68), and 1–4 (HR = 6.35, CI = 3.52–11.45) were greater during the post-breeding season (Table 3.3).

During diurnal hours, TPs for transitions 1–2 (HR = 0.69, CI = 0.58–0.83), 1–3 (HR = 0.31, CI = 0.27–0.38), and 1–4 (HR = 0.48, CI = 0.33–0.70) were less likely to occur than at night (Table 3.4).

The probabilities for the next state to occur revealed marked temporal segregation at individual feeding sites. For Prediction 1, TPs for transitions 1–2 and 1–3 were greater than 1–4 during diurnal and nocturnal hours in all seasons (Figure 3.2). Interestingly, TPs for transition 1–2 were consistently greater than 1–3 during diurnal hours (Figure 3.2). During nocturnal hours, TPs for transition 1–3 were greater than 1–2 during all seasons (Figure 3.2). For prediction 2, transitions 2–1 and 3–1 were greater than transitions 2–3 and 3–2 in all seasons during both diurnal and nocturnal hours (Figure 3.3).

Results of the DM indicated that the probability of the feeder being in a particular state differed by diel cycle and season (Table 3.5). During the pre-breeding season, the probability of a subordinate being present during day was 3.0x more likely than a dominant being present but did not differ at night (Figure 3.4). Additionally, the probability of an adult male being present at
the feeder was 5.9x greater at night than day during the pre-breeding season (Figure 3.4). During the breeding season, there was no difference for dominants and subordinates during diurnal or nocturnal hours (Figure 3.4). In the post-breeding season, subordinates were 1.7x more likely to be at the feeder than a dominant during diurnal hours but there was no difference during nocturnal hours (Figure 3.4).

**DISCUSSION**

Animals can reduce competitive interactions for a shared resource through temporal resource partitioning (Alanärä et al. 2001). However, how animals segregate along the temporal niche axis has been the focus of few studies, particularly in mammals (Adams and Thibault 2006). In the present study, dominants and subordinates within the same species showed a clear pattern of avoidance of the opposing cohort, with segregation varying according to season and the diel cycle.

Feeding site use was only similar for dominants and subordinates during the breeding season. However, feeding site use was also low for both groups during this season. Adult males increase diurnal movements from pre-breeding to breeding season (Tomberlin 2007, Webb et al. 2010) and it is during this time that males switch their focus from foraging to mate-searching behaviors (Lincoln et al. 1972, Beier and McCullough 1990, Tomberlin 2007). Furthermore, many adult male ungulates exhibit hypophagia during the breeding season (Warren et al. 1981, Chin and Brown 1984, Brivio et al. 2010) and visit feeding sites less than during the pre- and post-breeding seasons (Ozoga and Verme 1982). As mating activities are prioritized over foraging during the breeding season, the breeding males’ activity budget is directed away from foraging activity (Pelletier et al. 2009). Younger males, however, do not invest as heavily in breeding activities allowing them to place a higher priority on growth to improve future
opportunities for mating (Mysterud et al. 2008, Foley et al. 2015). Consequently, they are not as hypophagic as adult males during the breeding season (Mysterud et al. 2008).

Why subordinates also decreased feeding site visitation during the breeding season is unclear. With the lack of dominants at the sites, subordinates had greater access to the supplemental feed, but did not utilize it as heavily during the breeding season. Although yearling males do not exhibit the same intensity of search behavior as adult males, they do engage in mate-searching (Foley et al. 2015). Moreover, peak dispersal of yearling males coincides with the breeding season (Rosenberry et al. 1999). Therefore, some yearling males present during pre-breeding may have emigrated from the site, while immigrating yearling males would be naïve to the feeding site locations.

Adult females of many species are often harassed by breeding males (Clutton-Brock et al. 1992; Reale et al. 1996, Holand et al. 2006). Harassment can lead to poorer body condition (Holand et al. 2006) and even direct mortality (Reale et al. 1996). Therefore, spatially and temporally avoiding breeding males is beneficial for females when not in estrus, which may explain why feeding site use was lowest for females during the breeding season.

During the post-breeding season, males may be in poor physical condition, making abundant, high-energy food sources very profitable patches at which to forage. However, agonistic interactions are energetically expensive (Appleby 1980) and defending the feeding site from subordinates during this time would lessen the profitability of the resource. Likewise, testosterone levels are lower during the post-breeding season (Chin and Brown 1984, Miller et al. 1987) making aggressive behaviors less likely (Lincoln et al. 1972). Together, energy conservation and lowered aggression by adult males may explain why we saw less temporal segregation in the post-breeding season.
Dominance status clearly influenced temporal patterns in feeding site use. Adult male occurrences at the feeding sites were lower during diurnal periods, particularly during the pre-breeding season. The pattern of temporal partitioning whereby subordinates were more likely to be at the feeding sites during diurnal hours has obvious implications for human-induced mortality. Although hunting pressure was minimal on our site, in most of the region hunting is responsible for the majority of deer mortality (Dusek et al. 1992), especially in areas where large carnivores have been extirpated. On our study site, predation risk from carnivores and hunters was minimal because hunting pressure was low and bobcats and coyotes are not efficient predators of adult deer. Previous research at the site demonstrated that no sex-age class altered vigilance levels at feeding sites according to the diel cycle (Stone et al. in review). Therefore, deer may not have focused their anti-predator behaviors toward a specific predation threat.

Landscapes with multiple predators that differ in their hunting mode, add complexity to predator avoidance behaviors in these systems (Lone et al. 2014). Increased risk from one predator may cause behavioral shifts that increase their exposure to other potential predators. For example, Crosmary et al. (2012) showed that African ungulates shifted their activity times at waterholes in response to predation risk from human hunters, even at the expense of increased exposure to non-human predators. However, there remains a need to investigate how behavioral responses to predation risk at concentrated resources manifest in realized survival rates for each sex-age class, in addition to the indirect effects on prey.

Our study illustrates how patterns in temporal resource partitioning at feeding sites may influence relative risk to different sources of mortality. Subordinates used the shared resource at similar rates, but the pattern of temporal partitioning evidently would make subordinates more susceptible to human predation. Further research is needed to determine if an increase in hunting
pressure acts to compress temporal partitioning at feeding sites and how the resulting temporal patterns affect predation risk for dominant and subordinate cohorts.

ACKNOWLEDGEMENTS

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LITERATURE CITED


Tomberlin, J. W. 2007. Movement, activity, and habitat use of adult male white-tailed deer at Chesapeake Farms, Maryland, USA. M.S. thesis, North Carolina State University, Raleigh, NC, USA.


Figure 3.1 Transition diagram for multi-state model used to estimate probability of feeding sites transitioning from one state to another state, or the probability of the feeding site staying in the same state. There were 4 possible states (States 1–4) that a feeding site could be in during any given hour. State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present.
Table 3.1 Predictions and interpretations for transition probabilities.

<table>
<thead>
<tr>
<th>Prediction</th>
<th>State Transitions</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1–2 = 1–3 = 1–4</td>
<td>No temporal segregation</td>
</tr>
<tr>
<td>2</td>
<td>2–3 = 2–1</td>
<td>No temporal segregation</td>
</tr>
<tr>
<td></td>
<td>3–2 = 3–1</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present
Table 3.2  Hazard ratios (HR) and 95% confidence intervals for white-tailed deer supplemental feeding sites in Harris County, GA (2013–2014) during the pre-breeding season (13 September – 25 October) as compared to the breeding season.

<table>
<thead>
<tr>
<th>Transition</th>
<th>HR</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>State 1 - State 2</td>
<td>1.61</td>
<td>1.25</td>
<td>2.08</td>
</tr>
<tr>
<td>State 1 - State 3</td>
<td>1.77</td>
<td>1.39</td>
<td>2.25</td>
</tr>
<tr>
<td>State 1 - State 4</td>
<td>1.87</td>
<td>0.97</td>
<td>3.63</td>
</tr>
<tr>
<td>State 2 - State 1</td>
<td>0.88</td>
<td>0.68</td>
<td>1.15</td>
</tr>
<tr>
<td>State 2 - State 3</td>
<td>0.65</td>
<td>0.25</td>
<td>1.70</td>
</tr>
<tr>
<td>State 2 - State 4</td>
<td>1.82</td>
<td>0.39</td>
<td>8.57</td>
</tr>
<tr>
<td>State 3 - State 1</td>
<td>0.78</td>
<td>0.61</td>
<td>0.98</td>
</tr>
<tr>
<td>State 3 - State 2</td>
<td>1.81</td>
<td>0.39</td>
<td>8.43</td>
</tr>
<tr>
<td>State 3 - State 4</td>
<td>2.23</td>
<td>0.48</td>
<td>10.30</td>
</tr>
<tr>
<td>State 4 - State 1</td>
<td>1.11</td>
<td>0.50</td>
<td>2.47</td>
</tr>
<tr>
<td>State 4 - State 2</td>
<td>0.80</td>
<td>0.25</td>
<td>2.62</td>
</tr>
<tr>
<td>State 4 - State 3</td>
<td>0.82</td>
<td>0.28</td>
<td>2.38</td>
</tr>
</tbody>
</table>

*State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present*
Table 3.3 Hazard ratios (HR) and 95% confidence intervals for white-tailed deer supplemental feeding site in Harris County, GA (2013–2014) during the post-breeding season (28 November – 3 January) as compared to the breeding season.

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>State 1 - State 2</td>
<td>2.91</td>
<td>2.28</td>
<td>3.71</td>
</tr>
<tr>
<td>State 1 - State 3</td>
<td>2.93</td>
<td>2.32</td>
<td>3.68</td>
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<td>State 1 - State 4</td>
<td>6.35</td>
<td>3.52</td>
<td>11.45</td>
</tr>
<tr>
<td>State 2 - State 1</td>
<td>0.86</td>
<td>0.67</td>
<td>1.10</td>
</tr>
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<td>State 2 - State 3</td>
<td>1.26</td>
<td>0.55</td>
<td>2.88</td>
</tr>
<tr>
<td>State 2 - State 4</td>
<td>2.44</td>
<td>0.56</td>
<td>10.64</td>
</tr>
<tr>
<td>State 3 - State 1</td>
<td>0.75</td>
<td>0.60</td>
<td>0.94</td>
</tr>
<tr>
<td>State 3 - State 2</td>
<td>3.60</td>
<td>0.85</td>
<td>15.23</td>
</tr>
<tr>
<td>State 3 - State 4</td>
<td>2.60</td>
<td>0.60</td>
<td>11.26</td>
</tr>
<tr>
<td>State 4 - State 1</td>
<td>1.33</td>
<td>0.64</td>
<td>2.78</td>
</tr>
<tr>
<td>State 4 - State 2</td>
<td>0.97</td>
<td>0.33</td>
<td>2.82</td>
</tr>
<tr>
<td>State 4 - State 3</td>
<td>0.69</td>
<td>0.26</td>
<td>1.83</td>
</tr>
</tbody>
</table>

*aState 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present*
Table 3.4 Hazard ratios (HR) and 95% confidence intervals for white-tailed deer supplemental feeding site in Harris County, GA during diurnal hours as compared to nocturnal hours.

<table>
<thead>
<tr>
<th>Transition</th>
<th>HR</th>
<th>L</th>
<th>U</th>
</tr>
</thead>
<tbody>
<tr>
<td>State 1 - State 2</td>
<td>0.69</td>
<td>0.58</td>
<td>0.83</td>
</tr>
<tr>
<td>State 1 - State 3</td>
<td>0.32</td>
<td>0.27</td>
<td>0.38</td>
</tr>
<tr>
<td>State 1 - State 4</td>
<td>0.48</td>
<td>0.33</td>
<td>0.70</td>
</tr>
<tr>
<td>State 2 - State 1</td>
<td>0.96</td>
<td>0.80</td>
<td>1.15</td>
</tr>
<tr>
<td>State 2 - State 3</td>
<td>0.89</td>
<td>0.49</td>
<td>1.62</td>
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<tr>
<td>State 2 - State 4</td>
<td>0.86</td>
<td>0.39</td>
<td>1.90</td>
</tr>
<tr>
<td>State 3 - State 1</td>
<td>1.11</td>
<td>0.93</td>
<td>1.33</td>
</tr>
<tr>
<td>State 3 - State 2</td>
<td>0.71</td>
<td>0.32</td>
<td>1.58</td>
</tr>
<tr>
<td>State 3 - State 4</td>
<td>1.18</td>
<td>0.53</td>
<td>2.63</td>
</tr>
<tr>
<td>State 4 - State 1</td>
<td>0.87</td>
<td>0.55</td>
<td>1.36</td>
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<tr>
<td>State 4 - State 2</td>
<td>0.88</td>
<td>0.43</td>
<td>1.83</td>
</tr>
<tr>
<td>State 4 - State 3</td>
<td>1.19</td>
<td>0.59</td>
<td>2.39</td>
</tr>
</tbody>
</table>

*State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present*
Figure 3.2 Probability for a feeding site to transition from State 1 – State 2 (solid circle), State 1 – State 3 (hollow circle), and State 1– State 4 (triangle) during diurnal and nocturnal hours. State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present. Transition probability for transitions from State 1– State 2 was greater than State 1– State 3 and State 1– State 4 during diurnal hours in all seasons. During nocturnal hours, the transition probability for State 1 – 3 was greater than State 1 – 2 and State 1 – 4 in all seasons.
Figure 3.3 Probability for a feeding site to transition from State 2 – State 1 (solid circle), State 2 – State 3 (hollow circle), State 3 – State 1 (triangle), and State 3 – State 2 (hollow triangle) during diurnal and nocturnal hours. State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present. Transition probability for transitions from State 2 – State 1 was greater than State 2 – State 3 during diurnal and nocturnal hours in all seasons. Transition probability for transitions from State 3 – State 1 was greater than State 3 – State 2 during diurnal and nocturnal hours in all seasons.
Figure 3.4 Probability that a feeding site was in State 2 (subordinate present), State 3 (dominant present), or State 4 (subordinate and dominant present) during diurnal and nocturnal hours in the pre-breeding, breeding, and post-breeding seasons. During the pre- and post-breeding seasons, subordinates were more likely than dominants to be at a feeding site during diurnal hours. During all seasons, dominants and subordinates were equally likely to be at a feeding site during nocturnal hours.
Table 3.5 Estimates from Markov chain Monte Carlo generalized linear mixed model predicting the probability of a supplemental feeding site being in 1 of 4 states during the pre-breeding, breeding, and post-breeding seasons during diurnal and nocturnal hours.

<table>
<thead>
<tr>
<th></th>
<th>Posterior Mean</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>pMCMC*</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-4.046</td>
<td>-4.242</td>
<td>-3.883</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state2:breed:diurnal(^a)</td>
<td>-0.644</td>
<td>-0.828</td>
<td>-0.391</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state3:breed:diurnal</td>
<td>-0.944</td>
<td>-1.317</td>
<td>-0.553</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state4:breed:diurnal</td>
<td>-0.831</td>
<td>-1.081</td>
<td>-0.639</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state2:post:diurnal</td>
<td>1.010</td>
<td>0.861</td>
<td>1.165</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state3:post:diurnal</td>
<td>0.385</td>
<td>0.153</td>
<td>0.702</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state4:post:diurnal</td>
<td>-0.044</td>
<td>-0.163</td>
<td>0.132</td>
<td>0.454</td>
</tr>
<tr>
<td>state2:pre:diurnal</td>
<td>0.212</td>
<td>0.067</td>
<td>0.389</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state3:pre:diurnal</td>
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<td>-1.417</td>
<td>-0.752</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state4:pre:diurnal</td>
<td>-1.128</td>
<td>-1.318</td>
<td>-0.831</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state2:breed:nocturnal</td>
<td>0.112</td>
<td>-0.084</td>
<td>0.307</td>
<td>0.328</td>
</tr>
<tr>
<td>state3:breed:nocturnal</td>
<td>-0.170</td>
<td>-0.515</td>
<td>0.210</td>
<td>0.430</td>
</tr>
<tr>
<td>state4:breed:nocturnal</td>
<td>-0.694</td>
<td>-0.837</td>
<td>-0.559</td>
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<tr>
<td>state2:post:nocturnal</td>
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</tr>
<tr>
<td>state3:post:nocturnal</td>
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<td>1.620</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state4:post:nocturnal</td>
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<td>&lt;0.001</td>
</tr>
<tr>
<td>state2:pre:nocturnal</td>
<td>0.926</td>
<td>0.751</td>
<td>1.091</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>state3:pre:nocturnal</td>
<td>1.052</td>
<td>0.875</td>
<td>1.266</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

\(^a\)Represent lower and upper 95\% credibility intervals

\(^\#\)Number of simulated cases that are >0 or <0 corrected for number of MCMC samples

\(^a\) State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present. Reference class is State 1.
CHAPTER 4

SPATIO-TEMPORAL RESPONSES OF WHITE-TAILED DEER TO BAITING

IN GEORGIA

ABSTRACT Baiting can alter natural movement patterns potentially affecting deer harvest susceptibility. However, it is unknown if hunters are more likely to encounter deer at bait sites than other parts of their home range, which demographic may be more susceptible to harvest at bait sites, and how harvest susceptibility changes throughout the hunting season. Therefore, we calculated daily utilization distributions (UDs) during legal hunting hours for 34 (22 males, 12 females) adult (≥2.5 years-old) deer instrumented with global positioning system (GPS) collars. We calculated the ratio of UD overlap with bait sites and systematically-sampled points (grid points) in their home range as a measure of relative harvest susceptibility (RHS) during the pre-breeding, breeding, and post-breeding seasons. Additionally, we monitored a subset (22) of bait sites with camera traps, and recorded photographic occurrences (POs) per site per day during legal hunting hours for adult males, yearling males, and adult females. Relative harvest susceptibility was greater at grid points than bait sites for adult males and females during all seasons (RHS<1). For adult females, RHS was greatest during the pre-breeding season ($\bar{X} \pm SE; 0.78 \pm 0.01$). Adult male RHS was greatest during the breeding (0.63 ± 0.02) and post-breeding (0.62 ± 0.02) seasons. POs were 41% greater for females during the post-breeding and pre-breeding seasons. Yearling male POs were 3x greater during the post-breeding season than the breeding season. Adult male POs were 3.9x greater during the post-breeding season than during other seasons. Our results demonstrate that hunting over bait may not improve hunter success rates and each sex-age class’ harvest susceptibility is dependent upon breeding phase. Managers should consider seasonal differences in sex-age class-specific harvest susceptibility when formulating harvest regulations.
INTRODUCTION

The use of bait to hunt animals as a strategy for increasing hunter success is controversial among hunters and the non-hunting public (Dunkley and Cattet 2003, Brown and Cooper 2006, Rudolph et al. 2006). Baiting engenders many biological concerns such as its potential to impact non-target species and enhance transmission of zoonotic diseases (Brown and Cooper 2006, Sorensen et al. 2014). Baiting may also alter natural movement patterns and spatial distribution of deer (Kilpatrick and Stober 2002, Brown and Cooper 2006, Milner et al. 2014) potentially leading to a change in hunter harvest rates.

Baiting can reduce shot distances and increase harvest rates in some instances (Synatzske 1981, Langenau Jr et al. 1985), but research on its efficacy at improving hunter success rates is inconclusive (Winterstein 1992, Van Deelen et al. 2006, Fleegle 2010, Kilpatrick et al. 2010). For example, Wisconsin researchers determined that following a ban on baiting in part of the state, deer harvest by archers declined only 0.1 deer/km² (Van Deelen et al. 2006). Similarly, the Pennsylvania Game Commission reported that there was no increase in harvest in an area where baiting was temporarily legalized (Fleegle 2010). In contrast, baiting has led to increased hunter harvest in some instances (Frawley 2002, Kilpatrick et al. 2010).

Research on the effects of baiting on harvest susceptibility for different demographics of white-tailed deer (Odocoileus virginianus) is limited. Darrow (1993) reported that temporal patterns in bait site visitation differed among sex and age classes with males being least visible during hunting hours. Additionally, Ruth and Shipes (2005) and Kilpatrick et al. (2010) reported that females were more likely to be harvested at bait sites than males.

Spatiotemporal movement patterns, as determined by resource-gaining and antipredator behaviors, affect deer harvest susceptibility (Karns et al. 2012) but the induced effects of baiting
on these behaviors, and therefore harvest susceptibility remain unknown. For large herbivores, baiting may enable them to maximize the net “profit” of energy intake by allowing them to meet their nutritional requirements by concentrating movements around a high-quality food source (Murden and Risenhoover 1993). In contrast to native forages that may be temporally and spatially limited, when offered ad libitum in a consistent location, the presence of bait reduces search time and can make movements more predictable.

Although baiting can influence movement patterns, there is little evidence that baiting affects home range size (Darrow 1993, Williams and DeNicola 2000, Kilpatrick and Stober 2002). However, baiting can affect space use within home ranges (Milner et al. 2014). A common response to the establishment of bait sites is for deer to shift core areas closer to bait or form a new core area nearer the bait site (Darrow 1993, Williams and DeNicola 2000, Kilpatrick and Stober 2002). Although bait sites may influence space use within home ranges, diurnal movement patterns may be more directly related to harvest susceptibility as deer are only available for harvest during legal hunting hours and bait site use is greatest at night (Darrow 1993). Additionally, diurnal use of bait sites may change as the hunting season progresses (Synatszke 1981). However, it is unknown if hunters are more likely to encounter deer at bait sites than elsewhere in their home range and how sex- and age-class specific harvest susceptibility at bait sites changes during the hunting season.

Therefore, our objectives for this study were to determine: (1) if deer are more susceptible to harvest at bait sites than other parts of their home range, (2) which sex and age classes may be more susceptible to harvest at bait sites, and (3) how harvest susceptibility changes throughout the season. We hypothesized that deer would be less susceptible to harvest at bait sites than other parts of their home range because bedding, rumination, and travelling to and
from feeding areas should cumulatively represent a greater proportion of a deer’s activity budget than foraging, especially when forage is concentrated and predictable (Garver et al. 2012, Echols et al. 2013). For males, we hypothesized that harvest susceptibility would be greatest during the breeding season as their diurnal movement rates generally increase during this time (Webb et al. 2010), and bait sites may serve as focal areas in which males search for estrous females (Foley et al. 2015). For females, we hypothesized that harvest susceptibility would decline from the pre- to post-breeding season (Synatzske 1981, Darrow 1993).

**STUDY AREA**

We conducted this study on a 1,619-ha property in Harris County, GA, USA (32.8023°N, −84.9049°W). Elevations ranged from 200 – 275m. Vegetation communities on the study site included a mixture of pine, pine-hardwoods, hardwood drainages, and open areas. Pine stands made up approximately 983 ha (61%) of the land cover and were comprised primarily of loblolly (Pinus taeda) and shortleaf pine (P. echinata). Hardwood stands constituted approximately 582 ha (36%) of the study site and were dominated by oak (Quercus spp.), hickory (Carya spp.), tulip-poplar (Liriodendron tulipifera), and sweetgum (Liquidambar styraciflua). Open areas included pasture, fallow fields, row crops, and cultivated wildlife openings. Recreational white-tailed deer hunting was allowed on the property from the second Saturday in September to 15 January. The property received minimal hunting pressure and approximately 10 (<1 deer per 160 ha) white-tailed deer were harvested annually. Non-human predators on the site included bobcats (Lynx rufus) and coyotes (Canis latrans).
METHODS

We captured 24 deer (13 males, 11 females) between January 2013 – July 2013 and an additional 9 males and 1 female January 2014 – June 2014. We fit each deer with a Lotek 7000MU GPS collar (Lotek Wireless Inc., Newmarket, Ontario, Canada) and marked them with a uniquely numbered ear tag (National Band and Tag Co., Newport, KY). We programmed collars to collect a location in the form of X, Y coordinates every 30 minutes. We estimated age (yearling or adult) for captured-deer using antler characteristics, body morphology, and tooth development and wear (Severinghaus 1949). We followed all animal use and handling protocols mandated by University of Georgia Animal Use and Care Committee (Permit #A2012 06-007-Y2-A1).

Bait Sites

We established 34 bait sites in a variety of vegetation communities across the study site and used shelled corn as an attractant. Bait was presented via trough-style feeders (trough), barrel feeders (barrel), or placed directly on the ground (ground). Feeders were established >2 weeks prior to data collection to allow deer to acclimate to the feeders. For bait placed on the ground, we allowed 1 week for deer to find the bait before data collection commenced.

From 13 September – 3 January in 2013 and 2014, we used infrared cameras (Reconyx Hyperfire 550, Holmen, WI, USA) to observe visitation rates at 22 of the bait sites. Cameras were mounted to a tree or post 3 – 4 m from the site and approximately 75 cm from ground level. Cameras collected photographs 24 hrs per day, with a 5-minute delay between successive photographs. We assigned each observed deer at the bait site to a sex-age class [adult male (≥2.5 years-old), yearling male (1.5 years-old), and adult female (≥1.5 years-old)] based on antler and body morphology (Richards and Brothers 2003), and recorded the time and date of the
photograph. We excluded photographs for which the sex-age class could not be determined. We checked camera sites at least once per week to replenish bait and to replace camera batteries and memory cards as needed.

**Experimental Design**

We divided the hunting season into 16 weeks and delineated pre-breeding, breeding, and post-breeding seasons based on conception data from the study site (Stickles et al. 2015): (1) Pre-breeding -- weeks 1–6 (13 September – 25 October); (2) Breeding -- weeks 7–11 (26 October – 27 November); and (3) Post-breeding -- weeks 12–16 (28 November – 3 January). We analyzed camera trap data for three days (Monday, Tuesday, and Wednesday) of each week. We calculated mean photographic occurrences (POs; Jacobson et al. 1997) per day during legal hunting hours for each week of the pre-breeding, breeding, and post-breeding seasons for each sex-age class.

We generated weekly dynamic Brownian Bridge Movement Models (dBBMMs, Kranstauber et al. 2012) for each deer using Package “move” (Kranstauber and Smolla 2016) in Program R (R Core Team 2014). We then created daily dBBMMMs during legal hunting hours (30 minutes prior to sunrise – 30 minutes following sunset) for each deer that had a bait site within its home range during that week. We overlaid a grid of equally-spaced (150 m) points (hereafter: grid points) over the entire study site and created 50-m buffers around bait sites and grid points. We then summed the portion of the daily utilization distribution (UD) overlapping each buffer and calculated mean overlap with each buffer type as a measure of harvest susceptibility; hereafter: relative harvest susceptibility (RHS). To determine if deer were more susceptible to harvest at a bait site than other portions of their home range, we calculated the
ratio of UD overlap with bait site and grid points (Figure 1). Values >1 indicated selection for bait sites and values <1 suggested avoidance.

To test our hypotheses, we generated a set of candidate models to test for seasonal, sex-age class, and annual differences in POs and RHS (Table 4.1). We used Akaike’s Information Criteria adjusted for small sample size (AICc) and considered any model with a ΔAICc value of ≤4 as a competing model (Burnham and Anderson 2002). We used model averaging for competing models and based our inferences on coefficients with 95% confidence intervals (CI) that did not include zero. We used the full average estimates for competing models (Burnham and Anderson 2002).

We modeled POs by season and year for each sex-age class using a generalized linear mixed model (GLMM) with a poisson distribution. We considered bait site and week random effects. For our RHS model, we used a linear mixed model (LMM) with a Guassian distribution and considered week and individual deer random effects.

RESULTS

In 2013, we collared 24 deer (13 males, 11 females) prior to the beginning of the hunting season. Three females and two males were harvested by hunters. Entering the 2014 hunting season, 19 males (10 collared in 2013) and 6 females (5 collared in 2013) were collared. Six males died during the hunting season due to the following causes: vehicle collisions (1), poaching (2), and hunter harvest (3). In 2013, seven of 11 (63.6%) females and 10 of 13 (76.9%) males had a bait site in their home range for at least one week of the hunting season. During 2014, 5 of 6 (83.3%) females and 19 of 19 (100%) males had a bait site in their home range for at least one week of the hunting season.
We collected a total of 6,994 photographs. Of those, 1,451 (20.7%) occurred during legal hunting hours. Photographs during legal hunting hours contained images of 673 adult females, 295 yearling males, and 679 adult males. Models that included both sex*age class and season were the best-fitting models for POs (Table 4.2). The GLMM revealed that POs were greatest for females during the post-breeding ($\bar{X} \pm SE; 0.65 \pm 0.06$) and pre-breeding ($0.65 \pm 0.04$) seasons (Figure 4.2). Yearling male POs were greater during the post-breeding ($0.36 \pm 0.02$) than breeding ($0.12 \pm 0.01$) season but did not differ during other seasons (Figure 4.2). Adult male POs were greater during the post-breeding ($1.11 \pm 0.60$) season than both the pre-breeding ($0.28 \pm 0.02$) and breeding ($0.29 \pm 0.02$) seasons (Figure 4.2). POs were similar between years (Table 3).

The model containing only sex*age class was the best fitting model for RHS (Table 4.2). RHS was greatest at grid points for adult males and females during all seasons (RHS<1). In our RHS model, the interaction between sex and season was significant (Table 4.4, Figure 4.3). For adult females, RHS was greater during the pre-breeding season ($0.78 \pm 0.01$) than the breeding ($0.34 \pm 0.01$) and post-breeding ($0.42 \pm 0.01$) seasons (Figure 4.3). Adult male RHS was greater during the breeding ($0.63 \pm 0.02$) and post-breeding ($0.62 \pm 0.02$) seasons than the pre-breeding ($0.26 \pm 0.02$) seasons (Figure 4.3).

**DISCUSSION**

Based on our results, deer may be less susceptible to harvest at bait sites than other portions of their home range. Both sexes appeared to avoid bait sites during legal hunting hours and at no point during the season did they select for bait sites over other areas available to them, suggesting that hunter success rates may be greater when hunting areas without a bait site. The concentration of activity around baiting sites has been demonstrated in white-tailed deer.
However, neither of these studies partitioned space use by time-of-day as in the present study. Our results suggest that during legal hunting hours, white-tailed deer do not concentrate their activity around bait sites.

Others have likewise found that baiting either decreased success rates or had no effect on harvest (Langenau Jr et al. 1985, Frawley 2002, Van Deelen et al. 2006, Fleegle 2010, Ruth and Shipes 2005). In contrast, Kilpatrick et al. (2010) reported that archery hunters using bait were more successful at harvesting antlerless deer than hunters that did not bait in an urban-suburban herd in Connecticut. However, their study occurred the first year that baiting was legalized and deer may have been naïve to the risk that bait sites present. Likewise, urban-suburban deer may be more habituated to human disturbance than deer in rural areas, such as our study site, and were possibly more likely to move and feed during legal hunting hours. Adult female POs were greatest during the pre- and post-breeding seasons but never exceeded 0.65 POs per day in all seasons. Relative harvest susceptibility was also greatest during the pre-breeding season. Beier and McCullough (1990) reported that females had the highest rate of diurnal activity in September and October.

Adult male presence at bait sites increased as the season progressed with greatest RHS during the breeding and post-breeding seasons. However, POs were lowest during the breeding and pre-breeding seasons. Increased RHS, but low POs during the breeding season may be related to males seeking receptive females at the bait sites, but not feeding there. Foley et al. (2015) demonstrated that when searching for mates during the breeding season, males will revisit “focal areas” where they have previously encountered females. Due to our low occurrence of POs and documented hypophagia by males during the breeding season (Moen 1978, Warren et
al. 1981, Chin and Brown 1984), we surmise that increased male RHS during the breeding season resulted from male search behavior.

The 3-fold increase in adult male POs during the post-breeding season likely resulted from the cessation of rutting activity and reduced nutritional condition at this time (Moen 1978, Warren et al. 1981, Beier and McCullough 1990). Adult male deer lose body mass from the breeding to post-breeding seasons (Warren et al. 1981) due to hypophagia and increased energy expenditure related to mate searching behaviors. A negative energy balance results in catabolism of fat reserves built up prior to the breeding season (Moen 1978). During the post-breeding seasons, bait sites become highly profitable patches at which to forage because deer can reduce energy costs by decreasing movements and exploit a consistent, high-energy food source.

Agencies charged with managing deer populations often structure hunting seasons to coincide with the breeding season (Stickles et al. 2015). Interestingly, in our study, POs were lowest during the breeding season across all sex-age classes. Koerth and Kroll (2000) noted that in Texas, deer used corn feeders less when native hard mast (Quercus spp.) was available. Acorns are a highly-preferred hard mast in the southeastern U.S. (Wentworth et al. 1992). On our study site, acorn availability coincides primarily with the pre-breeding and breeding season and may have affected bait site use during this time.

In other regions of the country, environmental conditions alter the seasonal availability of natural forage. Where snow cover limits forage availability, baiting may lead to increased hunter success rates. For instance, Kilpatrick et al. (2010) reported that archery hunters using bait harvested 8x more deer than non-baiters during January. Similarly, Kilpatrick and Stober (2002) reported greater core area shifts toward bait sites during winter, potentially making them more susceptible to management activities than during fall.
Additionally, deer densities can affect visitation rates and access to concentrated food resources (Grenier et al. 1999, Donohue et al. 2014). Density at our site likely did not change from 2013 to 2014, but changes in densities can have significant effects on bait site use. For example, Donohue et al. (2014) reported that in a high-density, captive herd, visitation was 29% greater than in low-density enclosures. Also, at greater densities, aggressive interactions increase and dominant sex-age classes may deny subordinates access to bait (Grenier et al. 1999, Donohue et al. 2014), therefore affecting sex-age class-specific harvest susceptibility at bait sites.

**MANAGEMENT IMPLICATIONS**

Although there is evidence that baiting may improve hunter success rates (Synatszke 1981, Kilpatrick et al. 2010) under certain conditions, the potential negative effects of baiting are likely to outweigh any realized increase in hunter success rates. We found that hunters are less likely to encounter deer at bait sites than other portions of their home range. Consequently, baiting may not be an effective management strategy for increasing harvest rates. Where legal, managers should consider differential sex- and age-class-specific seasonal harvest susceptibility when implementing harvest regulations.

**LITERATURE CITED**


Darrow, D. A. 1993. Effects of baiting on deer movement and activity. Thesis, Mississippi State University, Starkville, USA.


Table 4.1 Candidate models used to predict photographic occurrences (POs) and relative harvest susceptibility (RHS) for adult male (≥2.5 years-old), yearling male (1.5 years-old), and adult female (≥1.5 years-old) white-tailed deer at feeding sites in Harris County, GA, USA (September-January 2013 and 2014)

<table>
<thead>
<tr>
<th>Photographic Occurrences (POs)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1) sex-age class*season + year</td>
<td></td>
</tr>
<tr>
<td>2) sex-age class*season</td>
<td></td>
</tr>
<tr>
<td>3) sex-age class</td>
<td></td>
</tr>
<tr>
<td>4) season</td>
<td></td>
</tr>
<tr>
<td>5) year</td>
<td></td>
</tr>
<tr>
<td>6) NULL</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Relative Harvest Susceptibility (RHS)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1) sex*season + year</td>
<td></td>
</tr>
<tr>
<td>2) sex*season</td>
<td></td>
</tr>
<tr>
<td>3) sex</td>
<td></td>
</tr>
<tr>
<td>4) season</td>
<td></td>
</tr>
<tr>
<td>5) year</td>
<td></td>
</tr>
<tr>
<td>6) NULL</td>
<td></td>
</tr>
</tbody>
</table>

Predictor variables for POs were sex-age class (adult male, yearling male, adult female), season (pre-breed, breed, post-breed) and year.
Predictor variables for RHS were sex (adult male, adult female), season (pre-breed, breed, post-breed) and year.
Figure 4.1 Utilization distribution (UD) during legal hunting hours for an adult male on 2 October (A) and 31 December (B). We calculated the ratio of UD overlap with buffered bait sites and grid points to determine relative harvest susceptibility (RHS). RHS was lower for A (0.0) than B (1.5).
Table 4.2 Model selection results for models used to photographic occurrences (POs) and relative harvest susceptibility (RHS) for adult male (≥2.5 years-old), yearling male (1.5 years-old), and adult female (≥1.5 years-old) white-tailed deer at bait sites in Harris County, GA, USA (September-January 2013 and 2014). Models presented received the most support of our candidate models (ΔAICc <4).

<table>
<thead>
<tr>
<th>Sex-age Class</th>
<th>Model&lt;sup&gt;a&lt;/sup&gt;</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AIC Weight</th>
<th>Log-likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photographic Occurrences&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2) sex-age class*season</td>
<td>11</td>
<td>4746.04</td>
<td>0.00</td>
<td>0.73</td>
<td>-2361.91</td>
</tr>
<tr>
<td></td>
<td>1) sex-age class*season + year</td>
<td>12</td>
<td>4747.99</td>
<td>1.95</td>
<td>0.27</td>
<td>-2361.86</td>
</tr>
<tr>
<td>Relative Harvest Susceptibility&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2) sex*season</td>
<td>9</td>
<td>834.51</td>
<td>0.00</td>
<td>0.89</td>
<td>-408.03</td>
</tr>
</tbody>
</table>

<sup>a</sup>-Predictor variables for POs were sex-age class (adult male, yearling male, adult female), season (pre-breed, breed, post-breed) and year.

<sup>b</sup>-Predictor variables for RHS were sex (adult male, adult female), and season (pre-breed, breed, post-breed).
**Table 4.3** Parameter estimates for generalized linear mixed model (GLMM) predicting photographic occurrences (POs) for adult males, yearling males, and adult female white-tailed deer during the pre-breeding, breeding, and post-breeding seasons in Harris County, GA, USA, September–January, 2013–2014.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>Adjusted SE</th>
<th>z</th>
<th>P</th>
<th>lower CI</th>
<th>upper CI</th>
<th>*denotes 95% confidence interval does not contain zero</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.374</td>
<td>0.219</td>
<td>0.220</td>
<td>1.704</td>
<td>0.088</td>
<td>-0.805</td>
<td>0.056</td>
<td></td>
</tr>
<tr>
<td>Adult Female</td>
<td>0.273</td>
<td>0.120</td>
<td>0.120</td>
<td>2.276</td>
<td>0.023</td>
<td>0.038</td>
<td>0.508</td>
<td></td>
</tr>
<tr>
<td>Yearling Male</td>
<td>-0.844</td>
<td>0.165</td>
<td>0.165</td>
<td>5.122</td>
<td>&lt;0.001</td>
<td>-1.168</td>
<td>-0.521</td>
<td></td>
</tr>
<tr>
<td>Post-breed</td>
<td>1.418</td>
<td>0.220</td>
<td>0.220</td>
<td>6.435</td>
<td>&lt;0.001</td>
<td>0.986</td>
<td>1.849</td>
<td></td>
</tr>
<tr>
<td>Pre-breed</td>
<td>-0.004</td>
<td>0.229</td>
<td>0.229</td>
<td>0.018</td>
<td>0.986</td>
<td>-0.454</td>
<td>0.446</td>
<td></td>
</tr>
<tr>
<td>Adult Female*Post-breed</td>
<td>-0.805</td>
<td>0.142</td>
<td>0.143</td>
<td>5.644</td>
<td>&lt;0.001</td>
<td>-1.084</td>
<td>-0.525</td>
<td></td>
</tr>
<tr>
<td>Yearling Male*Post-breed</td>
<td>-0.299</td>
<td>0.190</td>
<td>0.190</td>
<td>1.571</td>
<td>0.116</td>
<td>-0.671</td>
<td>0.074</td>
<td></td>
</tr>
<tr>
<td>Adult Female*Pre-breed</td>
<td>0.572</td>
<td>0.166</td>
<td>0.166</td>
<td>3.439</td>
<td>0.001</td>
<td>0.246</td>
<td>0.897</td>
<td></td>
</tr>
<tr>
<td>Yearling Male*Pre-breed</td>
<td>0.854</td>
<td>0.213</td>
<td>0.214</td>
<td>3.998</td>
<td>&lt;0.001</td>
<td>0.435</td>
<td>1.272</td>
<td></td>
</tr>
<tr>
<td>Year (2014)</td>
<td>-0.021</td>
<td>0.134</td>
<td>0.134</td>
<td>0.153</td>
<td>0.878</td>
<td>-0.562</td>
<td>0.412</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.4 Parameter estimates for linear mixed-effects model predicting relative harvest susceptibility (RHS) for adult male (≥2.5 years-old) and female (≥1.5 years-old) white-tailed deer in Harris County, GA, USA, September–January, 2013–2014.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>lower CI</th>
<th>upper CI</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.289</td>
<td>0.121</td>
<td>2.390</td>
<td>0.053</td>
<td>0.523</td>
<td>*</td>
</tr>
<tr>
<td>Adult Male&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.306</td>
<td>0.142</td>
<td>2.155</td>
<td>0.030</td>
<td>0.582</td>
<td>*</td>
</tr>
<tr>
<td>Post-breeding&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.086</td>
<td>0.134</td>
<td>0.639</td>
<td>-0.176</td>
<td>0.348</td>
<td></td>
</tr>
<tr>
<td>Pre-breeding&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.423</td>
<td>0.139</td>
<td>3.053</td>
<td>0.153</td>
<td>0.694</td>
<td>*</td>
</tr>
<tr>
<td>Adult Male*Post-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.114</td>
<td>0.161</td>
<td>-0.709</td>
<td>-0.429</td>
<td>0.202</td>
<td></td>
</tr>
<tr>
<td>Adult Male*Pre-breeding&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-0.802</td>
<td>0.163</td>
<td>-4.926</td>
<td>-1.119</td>
<td>-0.483</td>
<td>*</td>
</tr>
</tbody>
</table>

<sup>a</sup>Reference class— Adult Female  
<sup>b</sup>Reference class— Breeding Season  
<sup>c</sup>Reference class— Adult Female*Breeding Season  
*denotes 95% confidence interval does not contain zero
Figure 4.2 Photographic occurrences (POs) during legal hunting hours for adult males, yearling males, and adult female white-tailed deer during the pre-breeding, breeding, and post-breeding seasons in Harris County, GA, USA, September – January, 2013–2014. Error bars represent 95% confidence intervals.
Figure 4.3 Relative harvest susceptibility (RHS) for adult male and female white-tailed deer during the pre-breeding, breeding, and post-breeding seasons in Harris County, GA, USA, September–January, 2013–2014. Values >1 indicate selection and values <1 suggest avoidance. RHS did not exceed 0.78 for either sex in any season.
CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

CONCLUSIONS

The results from this research suggest the following conclusions:

Chapter 2- Breeding Chronology and Social Interactions Affect Ungulate Foraging Behavior

1. Each adult sex-age class’ [mature male (≥3.5 years-old), immature male (≤2.5 years-old), and adult female (≥1.5 years-old)] feeding rate was influenced by breeding chronology.

2. Group size is an important consideration for all sex-age classes when foraging at a bait site. Feeding rates increased with increasing group size for each sex-age class (mature male, immature male, adult female, and fawn).

3. The presence of a mature male negatively affected the feeding of immature males demonstrating that conspecific aggression may impede resource-gaining for younger males.

4. Mature males and adult females showed marked temporal segregation at individual bait sites. We analyzed 6,994 camera trap images and documented very few (n=6) observations of mature males and females co-occurring in the same photograph.

5. Each sex-age class modulates vigilance levels in response to socio-sexual factors according to the unique pressures placed upon them by their reproductive status and social rank.
Chapter 3- Intraspecific temporal resource partitioning and implications for differential predation risk

1. Dominants (adult males; ≥2.5 years-old), and subordinates [(yearling males (1.5 years-old) and adult females (≥1.5 years-old)] showed a clear pattern of avoidance of the opposing cohort, with temporal segregation varying according to season and diel cycle (diurnal vs. nocturnal).

2. Feeding site use was lowest during the breeding season for dominants and subordinates. Possible mechanisms for this finding are mate searching by males, dispersal of yearling males, and temporal and spatial avoidance of males by non-estrous adult females.

3. Temporal segregation was lowest during the post-breeding season possibly due to reduced testosterone levels and physical condition of adult males following the breeding season.

4. During the pre-breeding season, subordinates were 3.0x more likely to be at a feeding site during diurnal hours than a dominant. Additionally, the probability of an adult male being present at a feeding site was 5.9x greater at night than day.

5. During the pre- and post-breeding seasons, subordinates were more likely than dominants to use a feeding site during diurnal hours. During all seasons, dominants and subordinates were equally likely to be at a feeding site during nocturnal hours.

Chapter 4- Spatio-temporal Responses of Deer to the Use of Bait during the Hunting Season

1. Based on GPS telemetry data, adult males and females were more susceptible to harvest in non-baited portions of their home range than at bait sites.

2. GPS-collared adult females were most susceptible to harvest at bait sites during the pre-breeding season.
3. GPS-collared adult males were most susceptible to harvest at bait sites during the breeding and post-breeding seasons.

4. Based on camera trap data, adult females were more likely to use bait sites during the pre- and post-breeding seasons. Adult and yearling males were most likely to use a bait site during the post-breeding season.

5. Hunting over bait may not improve hunter success rates and each sex-age class’ harvest susceptibility is dependent upon breeding phase.

**MANAGEMENT IMPLICATIONS**

1. Patterns in temporal resource partitioning at bait sites may influence relative risk to different sources of mortality (human and non-human predators).

2. Subordinates (yearling males and adult females) use bait sites at similar rates, but the pattern of temporal partitioning evidently would make subordinates more susceptible to hunter-induced mortality.

3. We found that hunters are less likely to encounter deer at bait sites than other portions of their home range. Consequently, baiting may not be an effective management strategy for increasing harvest rates.

4. Where legal, managers should consider differential sex- and age-class-specific seasonal harvest susceptibility when implementing harvest regulations.

5. There is a need to investigate how behavioral responses to predation risk at bait sites manifest in realized survival rates for each sex-age class, in addition to the indirect effects on prey.
6. Further research is needed to determine if an increase in hunting pressure modulates activity patterns at bait sites and how the resulting temporal patterns affect predation risk for dominant and subordinate cohorts.