GOBBLING ACTIVITY, ROOSTING BEHAVIOR, AND REPRODUCTIVE ECOLOGY OF EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*) IN THE PIEDMONT OF GEORGIA

by

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(Under the Direction of Michael J. Chamberlain)

ABSTRACT

I modeled 13,177 gobbles, behavioral data from 84 females during the reproductive season, and daily harvest of males to examine relationships between gobbling activity, hunting, and reproductive behaviors (laying, incubating) of females. I found gobbling activity on one day negatively influenced gobbling activity the following day. As the proportion of reproductively active females increased, predicted daily gobbling activity increased. Hunting activity negatively influenced predicted gobbling activity and the effect of hunting activity was disproportionately greater than the positive effect of female reproductive behaviors. I used spatial data from males to evaluate roost site selection and fidelity relative to habitat selection and hunting. I found males selected roost sites in pine and hardwood areas prior to hunting, but avoided pine after hunting began. Roost site fidelity was low prior to and during hunting. My findings suggest hunting may influence behavior in wild turkeys by suppressing gobbling activity and altering roost selection.

INDEX WORDS: Georgia, gobbling, hunting, *Meleagris gallopavo*, movement, reproductive phenology, roost site, wild turkey

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DEDICATION

I dedicate this thesis to my parents, Travis and Valerie, the rest of my family and friends, and my dogs, Gv-na and Copper, for their loving support and encouragement to chase my dreams by pursuing my M.S. Degree. Without everyone’s love and support, we would not have been able to do this.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Mating systems are defined by methods of mate acquisition, numbers of mates acquired, characteristics of bonding, and levels of parental care (Emlen and Oring 1977). Polygamy is a mating system defined by one or both sexes mating with multiple partners (Orians 1969, Emlen and Oring 1977). Polygamy evolved as a reproductive strategy to increase fitness when mates or necessary resources could be dominated. Under polygamy, one sex, generally the male, is removed from parental care responsibilities, and young are precocial (Orians 1969, Emlen and Oring 1977, Jennions and Petrie 1997, Olson et al. 2008). Secondary sex characteristics and behaviors used for direct or indirect intra-sex competition for mates or resources and tend to be pronounced in polygamous systems (Andersson and Simmons 2006, Hooper and Miller 2008, Maklakov et al. 2010, Weir et al. 2011).

Mate attraction is the use of specific traits, behaviors, or displays that lead to nonrandom mate acquisition (Andersson and Simmons 2006, Edward 2015). Strategies of mate attraction and acquisition vary across species; some simply alter behaviors during the reproductive period, whereas other strategies cause individuals to undergo changes that alter their appearance and behavior (Orians 1969, Emlen and Oring 1977, Jennions and Petrie 1997, Andersson and Simmons 2006, Weir et al. 2011). The magnitude and degree of alterations for mate attraction are dictated by many factors including predation risk, nutrition availability, population density, and many others. The most important factor affecting mate attraction behaviors is mate preference because of direct linkages between preferences and likelihood to successfully reproduce (Emlen and Oring 1977, Nowicki and Searcy 2004, Stewart et al. 2005, Zanette et al. 2006, Weir et al. 2011). In polygamous systems males generally undergo behavioral and physical changes during the reproductive season (Orians 1969, Jennions and Petrie 1997, Patricelli et al. 2002). Females select mates based on multiple cues associated with these behavioral and appearance changes in males (Candolin 2003, Edward 2015), and female mate selection is pronounced in polygamous species (Orians 1969, Jennions and Petrie 1997, Hooper and Miller 2008, Weir et al. 2011, Edward 2015). Males seek to provide signals as to their relative fitness to the opposite sex (Coleman et al. 2004).

Signaling is a form of communication within or among species through behaviors, vocalizations, displays, and scent marking (Emlen and Oring 1977, Jennions and Petrie 1997, Gosling and Roberts 2001, Larkin et al. 2002, Garamszegi et al. 2008). Mate acquisition is one primary reason that animals engage in signaling (Orians 1969, Emlen and Oring 1977, Andersson and Simmons 2006, Edward 2015), and signals are used as a way to communicate reproductive potential and increase opportunities for reproduction (Pomiankowski and Iwasa 1993, Olson and Owens 1998, Smith and Bird 2000, Gintis et al. 2001). The most common forms of signaling are displaying and vocalizations. Displaying uses physical attributes or behaviors to signal reproductive potential through visual cues (Théry and Endler 2001), and are commonly dances or forms of lekking (Alonso et al. 2012a). Conversely, calling is the use of auditory signaling to attract mates, usually in the form of a song (Nowicki and Searcy 2004, Ophir et al. 2010). The use of signals for mate acquisition can be in the form of intra-sexual competition, resource defense, or mate attraction.

Signaling can be energetically costly and can negatively influence survival by increasing predation risk (Berglund 1993, Berg et al. 2005, Stewart et al. 2005, Zanette et al. 2006). Risk-reward theory predicts that signaling must provide a greater reward than the associated costs to make the signal beneficial, and this reward is the opportunity to mate (Orians 1969, Olson and Owens 1998, Gintis et al. 2001, Hooper and Miller 2008). However, calling to attract a mate can pose risk for attracting a predator. For an animal to engage in signaling such as calling, there must be the perception of a greater chance of attracting mates than predators, or the behavior should cease. Risk associated with signaling often leads to signaling events being temporarily and spatial correlated to increased potential for mate acquisition (Luther 2009). When predation risk remains low, calling is predicted to be high, but when risk increases calling should decrease (Gintis et al. 2001, Hooper and Miller 2008).

Birds use several forms of signaling to achieve mate acquisition including plumage changes, calling, and displaying (Møller et al. 1998, Loyau et al. 2005). Forms of mate attraction used are driven by life history and features involved in intersexual selection (Orians 1969, Jennions and Petrie 1997, Nowicki et al. 1998, Nowicki and Searcy 2004). For instance, birds using denser habitats tend to display more frequently, whereas birds in open areas tend to call more (Orians 1969, Emlen and Oring 1977). Many species use a combination of these 2 signaling behaviors either simultaneously or during different phases of the reproductive season to attract mates (Pomiankowski and Iwasa 1993, Nowicki et al. 1998, Candolin 2003, Nowicki and Searcy 2004).

Wild Turkeys

The literature on Eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter turkey) is vast, but as it evolves and transforms gaps in knowledge are evident. Currently, most research focuses on females, but understanding the reproductive ecology of males is necessary for sustainable management of the species (Miller et al. 1997*a*, Healy and Powell 1999).

Turkeys are a polygamous species, wherein males exhibit specific signaling traits, behaviors, and displays to acquire multiple mates. Polygamy occurs in turkeys because males are free from parental responsibilities (Hubbard et al. 1999, Collier et al. 2009), females can be congregated to relatively small areas due to strong site fidelity (Grisham et al. 2008, Krakauer 2008), and females select males based off signals and secondary sex characteristics (Buchholz 1995). Theoretically, all females should be selecting for similar characteristics, so males with these traits are more likely to secure mates and therefore reproduce (Buchholz 1995, Badyaev et al. 1998, Théry and Endler 2001).

Male turkeys exhibit several forms of mate attraction to secure female selection (Buchholz 1995). For instance, males signal in the forms of displaying and calling (Miller et al. 1997*a*, Krakauer 2008), and coupled with displaying, males will alter their space use to increase their visibility to females (Hoffman 1991, Holdstock et al. 2005). Males call in the form of gobbling, which is a loud vocalization used to attract females and relay a male's reproductive potential. Both calling and displaying are costly forms of signaling (Moore et al. 1993, Wright and Vangilder 2005, Holdstock et al. 2006), as they have the potential to attract a mate but also predators. Hence, there is a risk and reward to the signaling male, the risk being predation and the reward reproduction (Humberg et al. 2009). Clearly, if the reward outweighs the risk, males should continue signaling for females (Zuk and Kolluru 1998), but if not, signaling should decrease or cease.

Calling

The main form of calling by male wild turkey is the gobble. Males gobble throughout the year at very low frequencies, but during the spring reproductive season gobbling activity increases dramatically to signal their fitness potential, attract females, and maintain pecking orders (Bevill Jr 1973, Healy 1992, Miller et al. 1997b, Healy and Powell 1999). Males gobble as a form of intra-sexual competition to establish dominance (Emlen and Oring 1977, Weir et al. 2011). Gobbling activity has extreme daily variations due to numerous factors but may exhibit ≥2 distinct peaks throughout the reproductive season. Typically, it is assumed he first peak in gobbling correlates with winter flock breakup and the second with nest incubation (Hoffman 1990, Miller et al. 1997*b*, Healy and Powell 1999, Lehman et al. 2005). Gobbling activity during flock break up is presumably associated with establishing dominance, whereas gobbling during peak nest incubation is presumably to attract the highest proportion of available, non-nesting females (Hoffman 1990). Conversely, other authors have shown that these peaks may only be assumed and not actually expressed in nature (Miller et al. 1997*a*). The lack of expression could be a result of the extreme daily variation in gobbling activity or from insufficient sampling resulting from use of standard road-based point counts and errors associated with this methodology (Wightman et al. 2019). Others have suggested that the lack of peaks in gobbling could be from additional factors influencing gobbling, such as female activity and male physiology, (Miller et al. 1997*a*), but these factors are poorly understood. Regardless, a thorough working knowledge of gobbling activity and gobbling chronology throughout the reproductive season is lacking.

Predator activity, including by humans, has potential to influence gobbling activity (Healy and Powell 1999, Zanette et al. 2006). Increased predator activity presumably translates to an increased predation risk to the individual who is calling. Increased predation risk to calling individuals can influence reproduction (Miller et al. 1998, Hughes et al. 2005), and affect behavior and physiology (Bateson and Bradshaw 1997, Roy and Woolf 2001, Coltman et al. 2003, Burke et al. 2008). Predation risk in the form of hunting is known to alter behavior in male turkeys (Gross et al. 2015*a*). In other species with similar breeding strategies and behaviors to turkeys, hunting pressure can negatively affect reproductive activity and alter breeding behavior (Suhonen et al. 1994, Larkin et al. 2002, Christianson and Creel 2007).

The acoustic adaptation hypothesis predicts calling frequency should be directly correlated to habitat conditions (Ey and Fischer 2009) that vary temporarily, seasonally, and daily. Furthermore, calling rate should reflect a bird's ability to propagate the landscape with a signal and increasing the potential for a mate to hear the call, which varies by vegetation characteristics (Boncoraglio and Saino 2007, Ey and Fischer 2009). Vegetation associations can be directly linked to the amount and rate of calling in various polygamous species (Nowicki et al. 1998, Creel et al. 2007b). Birds inhabiting open vegetation associations may call at lower frequencies and employ other signals such as displays to communicate; while in dense habitats individuals should call at greater rates to reach the intended target (Boncoraglio and Saino 2007). An understanding of calling in various vegetative associations can be important to understanding reproductive behavior in turkeys; it is expected that turkeys in open vegetation associations should engage in lower calling frequencies than turkeys in dense vegetation associations (Nowicki et al. 1998, Berg et al. 2005).

Managers require a thorough understanding of gobbling activity to aid in management of turkeys, including the setting of hunting seasons. Hunting is important for turkey population management because harvest dictates patterns of male mortality and can be used to observe population trends (Hubbard and Vangilder 2005, Wright and Vangilder 2005, Eriksen et al. 2010, Parent et al. 2015). Most hunting seasons are set based on tradition and the notion of 2 peaks in gobbling, one at the winter break up and one at the peak nest incubation of females (Miller et al. 1997*a*, Chamberlain et al. 2018, Isabelle et al. 2018). Hunting seasons are geared to coincide with the second peak of gobbling and maximize hunter satisfaction and harvest opportunity, while protecting females from illegal harvest and minimizing disturbance to nesting activity (Miller et al. 1997*a*, Lehman et al. 2005, Whitaker et al. 2005, Casalena et al. 2015). The understanding, occurrence, and cues associated with gobbling activity are relatively unknown, so nesting phenology is used to estimate peaks in gobbling and set seasons (Miller et al. 1997*a*, Lehman et al. 2005, Casalena et al. 2015). In addition to timing of breeding behavior, managers consider hunter input when setting seasons. Hunters generally rank hearing gobbles, seeing birds, and harvesting a bird as factors most influential to hunter satisfaction (Swanson et al. 2005, Casalena et al. 2011, Isabelle and Reitz 2015). With a greater understanding of factors influencing gobbling activity, managers could balance hunter input with turkey biology to best manage turkey populations and maintain stakeholder support (Flather et al. 2009, Harris 2010). To achieve this, managers need an understanding of factors influencing gobbling and how they relate to turkey reproduction.

Space Use

Male turkey behavior and movements shift throughout the year and vary between age classes (Godwin et al. 1990, Hoffman 1991). Male turkeys either alter space use during the reproductive period (Hoffman 1991) or alter behaviors within their ranges by changing movement patterns or habitat use (Grisham et al. 2008, Gross et al. 2015*b*) to increase signaling or mating opportunities. During the reproductive season, male movements tend to increase (Little and Varland 1981, Holdstock et al. 2005) to maximize exposure to available females, which decreases site fidelity (Hoffman 1991, Byrne et al. 2015). The extent of movement increases varies between age classes and subsets of the population (Godwin et al. 1990, Hoffman 1990, Godwin et al. 1992). For example, some have observed adults moving significantly more during spring than juveniles (Godwin et al. 1994), whereas others have observed the reverse (Hoffman 1991). The observed differences in movement patterns by age class could be related to population density and the ability for adults to congregate females or errors associated with previous methodology of data collection. Movement can also be affected by learned anti-predator behaviors. As turkeys learn high risk areas, they show increased movement in those areas to avoid predators; in low risk areas, movements tend to be reduced (Gross et al. 2015*a*).

Male turkeys use various areas of their home range differently throughout the year (Godwin et al. 1992, Miller et al. 1999). These shifts in home range tend to track seasonal resource requirements. During winter, males select home ranges that maximize availability to high energy food sources, which often include areas with mast producing hardwoods, riparian areas, and agricultural habitats (Godwin et al. 1992, Miller et al. 1999, Dunton et al. 2010, Isabelle et al. 2015). Home ranges also tend to be the smallest during these periods and are restricted to hardwood areas and valleys (Kelley et al. 1988, Rauch et al. 2010). During summer and fall, males tend to use areas of their home range to maximize foraging opportunities including increased preference for mature forest, especially pine and mixed mature forest (Godwin et al. 1992, Miller et al. 1999). In spring, home ranges shift from optimizing foraging to optimizing breeding opportunities. To optimize breeding opportunities and maximize exposure to females, adult males will select open areas such as fields and forest with relatively open understories (Ielmini et al. 1992, Miller et al. 1999, Holdstock et al. 2005). Patterns of male space use are well described, but often are contradictory in regards to size and seasonal shifts in space use. Ielmini et al. (1992) found male turkeys increased movement and used a greater portion of their home range during the reproductive period, presumably to increase opportunities to attract females. Conversely, Grisham et al. (2008) noted that male turkeys did not shift movement patterns or use space within their home range differently during the reproductive season.

Methodology

Historically, auditory point counts were used to monitor gobbling activity. Point counts often suffer from biases associated with variability in observer abilities, manpower requirements, and lack of replication (Lint et al. 1995, Healy and Powell 1999). Furthermore, point count data are typically too coarse to address hypotheses associated with factors influencing gobbling activity, such as time of day, time of year, and female availability (Miller et al. 1997*a*). The development of Autonomous Recording Units (ARUs) has potential to allow for non-biased research and more standardized data collection. The ARUs also allow for gobbling to be recorded at multiple locations simultaneously for preset periods (Colbert et al. 2015). With continuous sampling and removal of observer bias, variations in gobbling activity can be more precisely described.

Likewise, the use of Very High Frequency (VHF) radio transmitters to monitor wild turkeys has yielded considerable information on movements, space use, and resource selection. However, VHF telemetry suffers from various biases related to triangulation errors and observer effort and reduced rates of relocations throughout the day. Recently, the advent of Global Positioning Systems (µGPS) transmitters to monitor wild turkeys allows vast numbers of relocations on individuals, with more precise location data free of observer bias (Collier and Chamberlain 2011, Guthrie et al. 2011).

With advancements in GPS transmitters and ARUs, we were able to examine how female reproductive behaviors influence gobbling chronology and how male movement and habitat characteristics influence gobbling activity of eastern wild turkeys. The data used in this thesis are from 2 study sites in the Piedmont region of Georgia. Cedar Creek WMA is a large forested area with limited forest and habitat management with extensive hunting activity. B. F. Grant WMA is a smaller area with forested habitats juxtaposed to open habitats, with reduced hunting activity. Chapter 2 describes gobbling chronology in relation to nesting phenology of females, more specifically laying and incubation on both sites. Chapter 3 describes how male movement and habitat influence gobbling activity. The final chapter provides conclusions and management implications.

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CHAPTER 2

HUNTING AND NESTING PHENOLOGY DRIVE GOBBLING OF EASTERN WILD TURKEYS (*MELAGRIS GALLOPAVO SILVESTRIS*)[1]

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[1] Wakefield, C. T., P. H. Wightman, J. A. Martin, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. To be submitted to The Condor: Ornithological Applications.

Abstract

Wild turkeys (*Meleagris gallopavo*) use a polygynous mating system whereby males engage in multiple courtship behaviors, including vocalizations (gobbling) to attract females. Males must balance the risk of courtship behaviors with the reproductive potential of each courtship behavior. Male turkeys are primarily hunted during the reproductive period; hence the associated risk of courtship behaviors is increased. Many state agencies attempt to set hunting season frameworks that maximize hunter satisfaction by allowing hunting when gobbling activity is greatest and most females are theoretically incubating nests, but the relationship between gobbling activity and nesting phenology is unclear. We used autonomous recording units and global positioning systems (GPS) transmitters to monitor gobbling activity by male turkeys and reproductive behaviors of female turkeys in the Piedmont region of Georgia, USA. We modeled 13,177 gobbles and behavioral data from 84 females during the reproductive season, along with daily harvest of males by hunters using a state space model to examine relationships between daily gobbling activity, hunting activity, and reproductive behaviors (laying, incubating) of females. We observed a weak negative relationship between daily gobbling activity and gobbling activity the following day. As the reproductive season progressed gobbling activity decreased. However, as the proportion of females engaged in reproductive behaviors increased, expected daily gobbling activity increased. Conversely, we observed that hunting activity had a negative effect on daily gobbling activity, and the effect of hunting activity was disproportionately larger than the effect of female reproductive behaviors. Our findings suggest that predation risk via hunting activity by humans is an important determinant of gobbling activity by males, and that this predation risk may have mediating effects on the mating system of wild turkeys.

Introduction

Birds use various forms of signaling to acquire mates, including plumage changes, calling, and displaying (Møller et al. 1998, Loyau et al. 2005). Signals used in mate attraction are driven by life history strategies and reinforced through intersexual selection (Orians 1969, Jennions and Petrie 1997, Nowicki et al. 1998, Nowicki and Searcy 2004). Many species use a combination of signaling behaviors either simultaneously or during different phases of the reproductive season to attract mates and ultimately increase breeding opportunities (Pomiankowski and Iwasa 1993, Nowicki et al. 1998, Candolin 2003, Nowicki and Searcy 2004). Combinations of signaling behaviors vary greatly with some species such as monogamous birds using subtle signals such as slight changes in behaviors and elevated rates of calling while other species such as lekking and exploded lekking species may engage in more extreme behavioral changes such as competitive displays and greatly increased calling (Emlen and Oring 1977, Dunn et al. 2001, Alonso et al. 2012, Cornec et al. 2014). The patterns of signaling and displays used for mate attraction could drive the phenotypic differences between males and females (Emlen and Oring 1977).

Signals used in mate attraction should communicate reproductive potential and increase mating opportunities (Emlen and Oring 1977, Pomiankowski and Iwasa 1993, Gintis et al. 2001, Andersson and Simmons 2006, Edward 2015). In lekking and exploded lekking species, sexual selection is often facilitated by elaborate courtship displays and calling (Morales et al. 2001, Cornec et al. 2017). Signals are designed to express fitness benefits to females and establish dominance among males (Orians 1969), and females select mates using cues of male status conveyed through signals (Emlen and Oring 1977, Alonso et al. 2012). Therefore, females are selecting males based off signals and males are expected to adjust signaling frequencies at least partially in response to female behaviors (Orians 1969, Cox and Le Boeuf 1977). Previous authors have noted 2 primary ways in which female behaviors are believed to influence signaling frequencies of males. First, as females become reproductively active and/or fertile, males increase rates of competition and thus signaling, for breeding opportunities (Birkhead et al. 1987, Montgomerie and Thornhill 1989). Many bird species can store sperm and intense periods of reproductive activity often occur immediately before and while females are fertile (Brillard and Bakst 1990, Khillare et al. 2018). The last male to copulate with a female before egg production begins has improved chances of representation in the clutch, so as females enter periods of fertility or egg laying male signaling could increase (Birkhead et al. 1987, Brillard and Bakst 1990). Second, as numbers of available females decrease with onset of incubation, operational sex ratios skew greatly towards males, and male competition for remaining available females should increase (Weir et al. 2011). As male competition increases, frequency of courtship displays and signaling should likewise increase until some threshold when these displays are no longer profitable (Emlen and Oring 1977).

Signaling can be energetically costly and negatively influence survival of males by increasing predation risk (Berglund 1993, Berg et al. 2005, Stewart et al. 2005, Zanette et al. 2006), and predation risk can alter reproductive behaviors and strategies (Forsgren and Magnhagen 1993, Candolin 1998). Risk-reward theory predicts that signaling must provide a greater reward than the associated costs to make the signal beneficial, and the reward being opportunity to mate (Orians 1969, Olson and Owens 1998, Gintis et al. 2001, Hooper and Miller 2008). However, signaling to attract a mate can pose risk by attracting predators (Magnhagen 1991). For an individual to engage in signaling, there must be the perception of a greater chance of attracting mates than predators, or the individual should cease or alter the behavior. Thus, risk reward tradeoffs often lead to signaling events being temporarily and spatially correlated to periods of increased potential for mate acquisition (Luther 2009). When predation risk remains low, signaling is predicted to be high, but when risk increases signaling should decrease (Gintis et al. 2001, Hooper and Miller 2008).

Wild turkeys (*Meleagris gallopavo*) use a polygynous mating system, and males exhibit phenotypic characteristics driven by sexual selection such as fleshy head ornaments, hair like beards, and larger body size (Amadon 1959, Buchholz 1995;1997, Krakauer 2008). Males use elaborate courtship displays and vocalizations (gobbling) to attract females and maintain dominance hierarchies (Bevill Jr 1973, Healy 1992). Previous research suggested that rates of gobbling may increase during peaks in nest incubation (Bevill Jr 1973, Hoffman 1990, Miller et al. 1997, Norman et al. 2001, Lehman et al. 2005), whereas contemporary research has challenged these earlier works (Chamberlain et al. 2018). Gobbling chronology is used by agencies to establish regulatory frameworks, which dictate the timing of male harvest (Little et al. 2000, Swanson et al. 2005, Isabelle and Reitz 2015). Furthermore, male wild turkeys are primarily hunted during the reproductive season, and increased risk associated with hunting can negatively influence gobbling (Kienzler et al. 1995, Norman et al. 2001, Wightman et al. 2019). Hence, research is needed to evaluate how female reproductive behaviors coupled with potential influences of hunting could influence gobbling by male wild turkeys. We hypothesized that female reproductive behaviors and predation risk through hunting could influence daily gobbling, therefore our objectives were to evaluate potential relationships between daily gobbling activity, hunting activity, and female reproductive behaviors. We predicted that daily gobbling activity would be positively associated with female reproductive behaviors, but negatively associated with hunting activity.

Study Area

We conducted research on B. F. Grant and Cedar Creek Wildlife Management Areas (WMA) and surrounding privately owned areas in the Piedmont region of Georgia. B. F. Grant WMA was located in Putnam County, Georgia, USA, approximately 8 miles northwest of Eatonton, Georgia. This 4,613-ha area was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and managed cooperatively with the Georgia Department of Natural Resources, Wildlife Resources Division (GADNR). B. F. Grant WMA was bisected by Big Indian Creek and the western boundary was formed by Little River. The property was comprised of managed forest and agricultural land for livestock. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted in rye grass (*Lolium* sp.). Forested areas consisted of loblolly pine (*Pinus taeda*) forests, mixed hardwood and pine forests, and hardwood lowlands containing white oak (*Quercus alba*), sweet gum (*Liquidambar styraciflua*), yellow poplar (*Liriodendron tulipifera*), hickory (*Carya* sp.), and other oak species (*Quercus* sp.). The understory was dominated by sweet gum, eastern redbud (*Cercis canadensis*), muscadine (*Vitis rotundifolia*,), flowering dogwoods (*Cornus florida*), and briars (*Rubus* sp.). Forest management was primarily through patch cuts, thinning, and prescribed fire. The areas surrounding the property were predominately mixtures of pine forests and agricultural fields for livestock.

Cedar Creek WMA was located in Putnam County, Georgia, USA, approximately 10 miles southwest of Eatonton, Georgia. This area was owned by the U. S. Forest Service (USFS) and managed in partnership between the USFS and GADNR. Cedar Creek WMA was bisected by Big Cedar Creek and Murder Creek, and also contained portions of Glady Creek, Cedar Creek, and Badger Creek. The site was composed of managed loblolly pine forests, mixed hardwood and pine forests, hardwood valleys containing mostly white oak, sweet gum, yellow poplar, hickory (*Cary asp*.), and other oak species, and small openings for wildlife. The understory composition was similar to that on B. F. Grant WMA. The forests of Cedar Creek WMA were primarily managed through thinning and periodic (3- or 4-year return interval) dormant season fire (January through March). The land cover composition of B. F. Grant and Cedar Creek WMAs was 39.5% hardwood forests, 32.1% pine forests, 5.4% mixed forests, 19.8% open areas, 0.1% water, and 3.1% developed areas. Areas surrounding the property were predominately mixtures of pine forest and agricultural fields for livestock.

Both sites had annual spring turkey hunting seasons. The season on B. F. Grant WMA consisted of 3 hunting segments, which included an adult-child hunt from 25 March -2 April of 2017 and 24 March -1 April of 2018, an 80-person quota hunt from 3 April -9 April of 2017 and 2 April -8 April of 2018, and a general (open to the public) hunt from 10 April -15 May of 2017 and 9 April -15 May 15 of 2018. On Cedar Creek WMA, the season was a general (open to the public) hunt which opened on 25 March in 2017 and 24 March in 2018, and closed on 15 May of both years. The annual bag limit for both sites was 3 male wild turkey/hunter. All harvested males had to be reported to GADNR. The reported information from harvested males included location of harvest, and if the location of harvest was public property, also included the specific WMA.

Methods

We captured turkeys using rocket nets (Delahunt et al. 2010) during January-March 2017 and 2018. Captured birds were sexed following Pelham and Dickson (1992). All captured birds were banded with uniquely numbered aluminum rivet style leg bands. We radio-marked all females with backpack style GPS units (Guthrie et al. 2011) (Lotek Wireless, Newmarket, ON, Canada). We programmed GPS units to record locations hourly from 0500 through 2000 and one roost location at 2359 for the life of the units (Cohen et al. 2018).

We monitored radio-tagged turkeys >1 time per week from time of capture until the end of the reproductive season (late July) using 3-element handheld antennas and receivers (R2000, R4000; Advanced Telemetry Systems, Inc., Isanti, MN). We downloaded GPS locations remotely each week until evaluation of GPS locations showed the female visiting the same location daily (laying a clutch) or locations concentrated around a central location and did not significantly deviate for several days (incubating nest), at which point we began downloading locations ≥1 times weekly (Yeldell et al. 2017, Chamberlain et al. 2018, Wood et al. 2018). Throughout the course of the reproductive season, we classified females into reproductive phases, which included prenesting, laying, incubation, brooding, and post-nesting (Wood et al. 2018). For purposes of our study, we were only interested in whether females were laying or incubating nests (hereafter reproductively active). We determined laying dates based off the first estimated visit to the nest site from the GPS data (Yeldell et al. 2017, Chamberlain et al. 2018, Wood et al. 2018). When the date of first visit was undetermined, we used clutch size determined once the nest hatched or failed to estimate the onset of laying. If no eggs or insufficient egg shells were found, we assumed laying began 12 days prior to incubation (Yeldell et al. 2017). We determined a female to be incubating when the GPS locations did not deviate from a central location for several days (Yeldell et al. 2017). When a female began incubating, we monitored her daily until she left the nest site. Upon the female leaving the nest, we located the nest site to determine if the nest was successful (hatched ≥1 egg) or failed (nest abandoned, egg fragments, lack of eggs, or female mortality; Wood et al. 2018). After nest failure, we continued to monitor females for additional nest attempts. We considered a female to be post nesting after failure of the final nest attempt or brood loss.

We deployed 24 autonomous recording units (ARU; Song Meter, SM4 Digital Field Recorders, Wildlife Acoustics, Inc., Concord, MA) to collect ambient acoustic recordings from 1 March through 30 June. We constructed a 2 km grid of the study area and placed ARUs within each grid cell in areas predicted to have turkeys present based off field observations and prior research, which included hardwood stands, edges of fields or openings, managed pine stands, and areas near water or other riparian zones (Colbert 2013, Wightman et al. 2019). The land cover composition sampled by the ARUs (assuming a 207 m sampling diameter (Colbert et al. 2015)) was 34.6% hardwood forest, 37.3% pine forest, 5.1% mix forest, 20.3% open area, 0% water, and 2.6% developed areas. We also separated ARUs >2 km apart to prevent overlap in sampling. We placed microphones at a height of ~10 meters in pine trees to reduce interference associated with understory and midstory vegetation (Colbert et al. 2015). We set ARUs to collect data from 0500 hours to 1100 hours, which encompasses >85% of daily gobbling activity (Wightman et al. 2019).

We searched audio files for gobbles using the call recognition software (CRS) Raven Pro versions 1.4 and 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY) and methods described by Chamberlain et al. (2018) and Wightman et al. (2019). The CRS allowed gobbles to be assessed auditorily and visually. We created a call recognition file using the Limited Band Energy detector function to identify sounds ranging from 700 hz to 1275 hz and between 0.2 and 2.0 seconds in length with a 20% minimum occupancy and 10% noise ratio threshold in the range (Chamberlain et al. 2018, Wightman et al. 2019). The Limited Band Energy detector function created a selection of all potential gobbles. Due to expected high false positive rates (Colbert

2013), we visually and auditorily verified all potential gobbles. We stored selections identified as a gobble into a selection table, which included date and time (Chamberlain et al. 2018, Wightman et al. 2019).

We used harvest reports from GADNR to determine harvest on Cedar Creek and B. F. Grant WMAs. Harvest reports included WMA of harvest and date of harvest, which allowed us to evaluate potential effects of the removal of males during the hunting season on daily gobbling activity. We calculated the total harvest as the sum of harvest across both sites and both years. We also calculated the daily harvest as the number of males removed each day of the season across both sites during both years.

Our methods generated 3 time series datasets that were coupled spatially and temporally: 1) daily gobbling activity of males, 2) the presence or absence of hunting activity, and 3) the proportion of females exhibiting reproductive behaviors. Previous research has noted that both hunting and female behavior can influence male vocalizations (Bevill Jr 1973, Kienzler et al. 1995, Norman et al. 2001, Lehman et al. 2005), but the magnitude of effect is unknown. Therefore, we modeled our time series data to evaluate effects of stochasticity via hunting and reproductive behaviors of females on daily vocalizations of males. Assessing time series data requires models, such as state-space models, that account for correlated observations and preferably account for observation error. State-space models are hierarchical models that decompose time series of counts or other observations into a process variation and observation error (Kéry and Schaub 2012, Iijima et al. 2013, Osada et al. 2015). State-space models also separately account for process variations that result from stochasticity in parameters of interest. In essence, state-space models predict future states of a system probabilistically using a process model, based on information detailed in previous states of the same system.

We fitted the state-space model within the jagsUI package (Kellner 2015) of R (R Core Team, 2017) to estimate the effects of hunting and female reproduction on male gobbling activity. Observed daily gobbling was adjusted by cumulative removal of males using an offset term in the model, calculated from daily harvest compared to total harvest. Given parameters are on varying scales, we scaled reproductive behaviors by 2 standard deviations to allow direct comparison to the binary variable, hunting (Gelman 2008). We fit a Bayesian state-space model to daily gobbling data, which consisted of the following pair of equations:

$x_t = f\,(x_{t-1}) + \varepsilon_t$ equation 1

$y_t = f\,(x_t) + \eta_t$ equation 2

Equation 1 represents the process model for gobbling activity, with $\varepsilon_t \sim \textit{Normal}\,(0, \sigma^2_p)$ representing an error term that measures the process variance of gobbling activity not explained by $f\,(x_{t-1})$. The observation model in equation 2 links the process model of gobbling activity to the observed count data y_t while controlling for η_t, the observation or sampling error ($\eta_t \sim \textit{Normal}\,(0, \sigma^2_{obs})$). We used the discrete-time Gompertz model to relate equation 1 to predicted number of daily gobbles (N_t) using the approach outlined by Koons et al. (2015):

$\log\,(N_t) = x_t = x_{t-1} + e_{t-1} + \beta_{dailygobbling} + \beta_1\,(x_{t-1} + e_{t-1}) + X_{\mathrm{reproduction}}\,\beta_{\mathrm{reproduction}} + X_{\mathrm{hunting}}\,\beta_{\mathrm{hunting}} + \varepsilon_t$

equation 3

Where $e = \log\,[\mathrm{abs}\,(1 - (\mathrm{harvest}_t / \text{total harvest})]$ is the offset term, $\beta_{dailygobbling}$ is the mean growth rate of gobbling, β_1 is the coefficient of density dependence, $\beta_{\mathrm{reproduction}}$ is the coefficient for proportion of females in reproduction in matrix $X_{\mathrm{reproduction}}$, and β_{hunting} is the coefficient for hunting in matrix X_{hunting}. A vague normal prior with a mean of 0 and precision of 0.001 was used for each estimated parameter.

We used Markov chain Monte Carlo (MCMC) to estimate the posterior distributions of the model parameters. We generated three MCMC chains using a thinning rate of one, 75,000 iterations per chain, and 25,000 burn-in values. We inspected trace plots of the MCMC chains as an indicator of convergence. Furthermore, we used Gelman-Rubin statistic, $\hat{R}$, to check chain convergence (Gelman et al. 2004). $\hat{R}$ values are a measure of convergence derived by comparing variance between multiple chains to the variance within each chain. $\hat{R}$ values below 1.1 indicate model convergence and all estimated parameters in our model had $\hat{R}$ values ≤ 1.1.

Results

Using the 24 ARUs, we collected 5,629 days of recordings from 1 March through 30 June of 2017 and 2018. We processed 3,203,607 detections and positively identified 13,177 gobbles (Table 2.1). We observed an average of 275 gobbles per ARU per year and noted that 72% of gobbling activity occurred within 1 hour of sunrise (Figure 2.1). We observed most gobbles (63%) during March and noted that gobbling declined markedly from April (31%) through May (4%) both years (Figure 2.2).

We captured 84 female wild turkeys during 2017 (*n* = 43) and 2018 (*n* = 41). During 2017, 43 females incubated 58 nests. We noted laying behaviors from 7 March through 30 June of 2017 (Figures 2.3). The average date of initiation of laying behaviors was 14 April, and the median date of initiation of laying behaviors was 2 April during 2017. Earliest onset of incubation in 2017 was 20 March and incubation behaviors continued through 30 June (Figures 2.3). The mean date of initiation of incubation was 27 April and the median date of initiation of nest incubation was 15 April during 2017. During 2018, 41 females incubated 54 nests. We noted laying behaviors from 1 March to 30 June of 2018 (Figures 2.3). The average date of initiation of laying behaviors was 8 April, and the median date of initiation of laying behaviors was 31 March during 2018. Earliest onset of incubation in 2018 was 15 March and incubation behaviors continued through 30 June (Figures 2.3). During 2018 the mean date of nest incubation was 22 April and the median date of initiation of nest incubation was 14 April in 2018 (Figure 2.3). GADNR reported the harvest of 113 males during 2017 ($n = 51$) and 2018 ($n = 62$). Daily gobbling activity declined markedly after the onset of hunting, and also declined as number of males harvested increased (Figure 2.3).

The results from the state-space model indicated daily gobbling activity was negatively influenced by gobbling the previous day ($\beta = -0.48$, 95% CI = -0.74, -0.21) and daily gobbling activity generally declined throughout the reproductive season (Figure 2.4). The state-space model accurately predicted gobbling activity compared to our observed gobbling activity (Figure 2.4). Our results support our hypothesis that female reproductive behaviors and predation risk through hunting collectively influence daily gobbling. We observed a positive effect of female reproductive behaviors on predicted gobbling activity ($\beta = 1.09$, 95% CI = 0.27,1.95; Figures 2.5 and 2.6). Prior to hunting season, as the proportion of females engaged in reproduction increased the predicted daily decline in gobbling was reduced until the proportion of females in reproduction increased exceeded 0.40 ($r \geq 0$) at which point gobbling activity began to increase (Figure 2.5). During hunting season, the predicted rate of change in gobbling was always negative, but the rate of decline was less as the proportion of females engaged in reproduction increased (Figure 2.6). Biologically, this means that as the proportion of females in reproduction increases by 42%, we would expect daily gobbling activity to increase by a factor of 2.9 [exp (1.09)]. Conversely, we observed that hunting negatively influenced daily gobbling activity (β= -1.31, 95% CI = -2.58, -0.05; Figure 2.7). When hunting activity is present, we expect daily gobbling activity to decrease by a factor 3.7 [1/exp (-1.31)].

Discussion

Our findings support the hypothesis that female reproductive behaviors and predation risk through hunting influence daily gobbling activity. We noted a negative relationship between predicted gobbling activity relative to gobbling the previous day. Daily gobbling activity was positively related to the proportion of female turkeys exhibiting reproductive behaviors (laying, incubating nests). Conversely, daily gobbling activity was negatively related to the presence of hunting activity, and we noted that gobbling activity declined precipitously with the onset of hunting and removal of males via harvest. We offer that this finding is a consequence not only of the removal of vocal males from the landscape, but also elevated predation risk (hunting activity) prompting males to reduce vocalizations and adopt alternative strategies to secure reproductive opportunities. Collectively, our findings suggest that hunting activity is an important mediating effect on daily gobbling activity in the turkey population we studied.

Wild turkeys have pulsatile testosterone levels that result in day-to-day fluctuations in breeding behaviors (Bacon et al. 1991), and vocalizations associated with breeding activity are driven by changes in testosterone levels that increase markedly in spring (Lisano and Kennamer 1977, Wada 1981, Johnsen 1998, Fusani 2008). Testosterone levels in many species, including within the order Galliformes, oscillate temporally, which results in predictable fluctuations in calling activity throughout the breeding season (Wada 1981, Møller et al. 2005). Many behaviors in avian species synchronize (Evans and Patterson 1971) including calling and breeding behaviors (Stokes and Williams 1968, Fusani 2008), so we would expect synchronized calling and breeding behaviors to be a result of synchronized fluctuations in testosterone. Likewise, previous authors have noted these similar fluctuations in daily gobbling activity in wild turkeys (Chamberlain et al. 2018, Wightman et al. 2019), hence we were not surprised to observe a negative relationship between predicted daily gobbling activity relative to gobbling activity the previous day.

Previous studies have demonstrated positive correlations between the onset of nest initiation (laying) and gobbling activity (Kienzler et al. 1995, Miller et al. 1997, Chamberlain et al. 2018), similar correlations between peaks in gobbling activity and nest incubation (Hoffman 1990, Norman et al. 2001), and that lags between the onset of laying and peaks in gobbling activity may exist (Chamberlain et al. 2018). We modeled relationships between daily gobbling activity and the proportion of females exhibiting either laying or incubation behaviors and observed a positive relationship. We offer that the relationship between daily gobbling activity and the proportion of females exhibiting either laying or incubation behaviors relates to the receptivity and availability of females on the landscape as breeding season progresses. Male wild turkeys become receptive to breeding before females (Williams and Austin 1988, King and Millar 1995), and as females become receptive to copulation, signaling increases as males attempt to attract females and secure mating opportunities (Cox and Le Boeuf 1977, Emlen and Oring 1977, Montgomerie and Thornhill 1989). Fertile periods in birds typically cease with the fertilization of the last egg in the oviduct (Birkhead et al. 1987), which would fall within the laying sequence. Furthermore, although sperm storage facilitates sperm competition and allows birds to lay fertile eggs weeks after copulation (Birkhead and Møller 1992, Khillare et al. 2018), males can increase fitness by copulating with females prior to egg laying. Hence, male competition and signaling escalates presumably as males seek mating opportunities with females entering into the laying sequence, as copulating with these receptive females increases the likelihood the male will be represented in the clutch (Emlen and Oring 1977, Birkhead et al. 1987, Brillard and Bakst 1990). Likewise, male signaling may be influenced by the ratio of receptive females to males (Emlen and Oring 1977), and as numbers of receptive females declines with onset of incubation, competition amongst males and frequency of courtship displays (i.e., vocalizations) should increase (Weir et al. 2011). We note that operational sex ratios could become altered as females begin incubating nests, but these ratios also could become further skewed through removal of males via harvest while laying and onset of incubation are occurring.

Predation risk can negatively affect signaling and courtship displays (Lima 2009). Courtship behaviors like gobbling can increase predation risk because predators may also be attracted to calls (Burk 1982, Berglund 1993). Previous research has noted that males of various species may alter courtship displays in response to elevated predation risk (Hedrick 2000). Risk allocation hypothesis suggest that during periods of increased predation risk animals should allocate more efforts to antipredator efforts (Lima and Bednekoff 1999), and hunting activity can function as an intense, temporally variable form of elevated predation risk, and can alter individual behaviors (Crosmary et al. 2012, Bonnot et al. 2013). Because male wild turkeys are hunted primarily during their breeding season, hunting artificially increases predation pressures specifically on the male segment of the population (Humberg et al. 2009), which can influence behaviors of males. Indeed, elevated predation risk via hunting is known to suppress gobbling activity (Kienzler et al. 1995, Lehman et al. 2005, Wightman et al. 2019, this study) and influence male spatial behaviors (Gross et al. 2015).

Male wild turkeys are the only gamebird in the conterminous United States hunted specifically during peaks in reproductive activities (Chamberlain et al. 2018, Isabelle et al. 2018), and hunting is generally timed to expose hunters to periods when males are most vocal and gobbling activity is greatest (Miller et al. 1997, Lehman et al. 2005). Gobbling not only attracts females, but also serves to maintain established pecking orders and male dominance hierarchies (Healy 1992, Kienzler et al. 1995, Wightman et al. 2019). We offer that hunting potentially removes a segment of vocal males from the landscape, while also prompting remaining males to reduce gobbling (Lehman et al. 2005, Chamberlain et al. 2018), and in our study population, eventually cease gobbling well before the end of the reproductive season. Vocal males are theoretically more dominant individuals (Neumann et al. 2010, Bolt 2013), and removing them from the breeding population prior to peaks in onset of nest incubation could negatively influence fitness potential within the population (Ginsberg and Milner-Gulland 1994, Milner et al. 2007). Likewise, our observation that remaining males in the population cease gobbling early in the reproductive season suggests that remaining males must adapt alternative reproductive strategies to secure breeding opportunities (Burk 1982, Zuk and Kolluru 1998, Hedrick 2000).

Predation risk, whether real or perceived, is increasingly posited as a mechanism that produces cascading effects of predator presence and activity on prey populations (Laundré et al. 2010). Likewise, persistent influences of predation risk on individual behaviors may scale up to influence population dynamics (Creel et al. 2007, Matassa and Trussell 2011). Indeed, as predation risk increases and expanses of landscapes become riskier, factors such as resource availability may become less important in structuring prey populations than risk of predation (Laundré et al. 2014). Our findings contribute to a growing literature suggesting that human disturbance, hunting, and harvest can create changes in prey behavior that opposes adaptive responses to sexual selection (Ciuti et al. 2012), which has potential to outpace selective forces in regards to phenotypic, genetic, and life history traits (Hutchings and Baum 2005, Darimont et al. 2009). Human harvest of wild turkeys may be selective for desirable behavioral traits (i.e., aggressive and vocal males), as increased calling activity by males is widely known to most influence hunter satisfaction (Little et al. 2000, Casalena et al. 2011). We postulate the notable negative influence of predation risk through hunting on calling behavior of males could be an important influence on the mating system of wild turkeys (Allendorf and Hard 2009).

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Table 2.1: Summary of detections, gobbles, and false positive rates obtained from 24 autonomous recording units used to determine daily gobbling activity of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) on B. F. Grant Wildlife Management Area (BFG) and Cedar Creek Wildlife Management Area (CC) in the Piedmont region of Georgia, USA 2017-2018.

Site	Year	Detections	Gobbles	Gobbles (%)	False Positives (%)	Gobbles/unit
CC	2017	874052	4103	0.47	99.53	256.44
CC	2018	1145534	3868	0.34	99.66	241.75
BFG	2017	603826	3396	0.56	99.44	424.5
BFG	2018	580195	1810	0.31	99.69	226.25

Table 2.2: Parameters and associated means and uncertainty from state space model for the relationship between daily gobbling activity (daily gobbling), female reproductive behaviors (reproduction), and hunting activity (hunt), and variance of observed and predicted (process) gobbling by male Eastern wild turkeys (*Meleagris gallopavo silvestris*) on Cedar Creek and B. F. Grant Wildlife Management Areas Georgia, USA during 2017-2018.

Parameters	Mean	SD	2.5%	50%	97.5%
Observation variance	0.441	0.321	0.006	0.424	1.085
Process variance	0.828	0.392	0.169	0.820	1.543
Intercept	2.644	0.985	0.767	2.677	4.469
Daily gobbling	-0.480	0.141	-0.737	-0.486	-0.208
Hunt	-1.305	0.668	-2.584	-1.313	-0.050
Reproduction	1.085	0.444	0.268	1.080	1.952

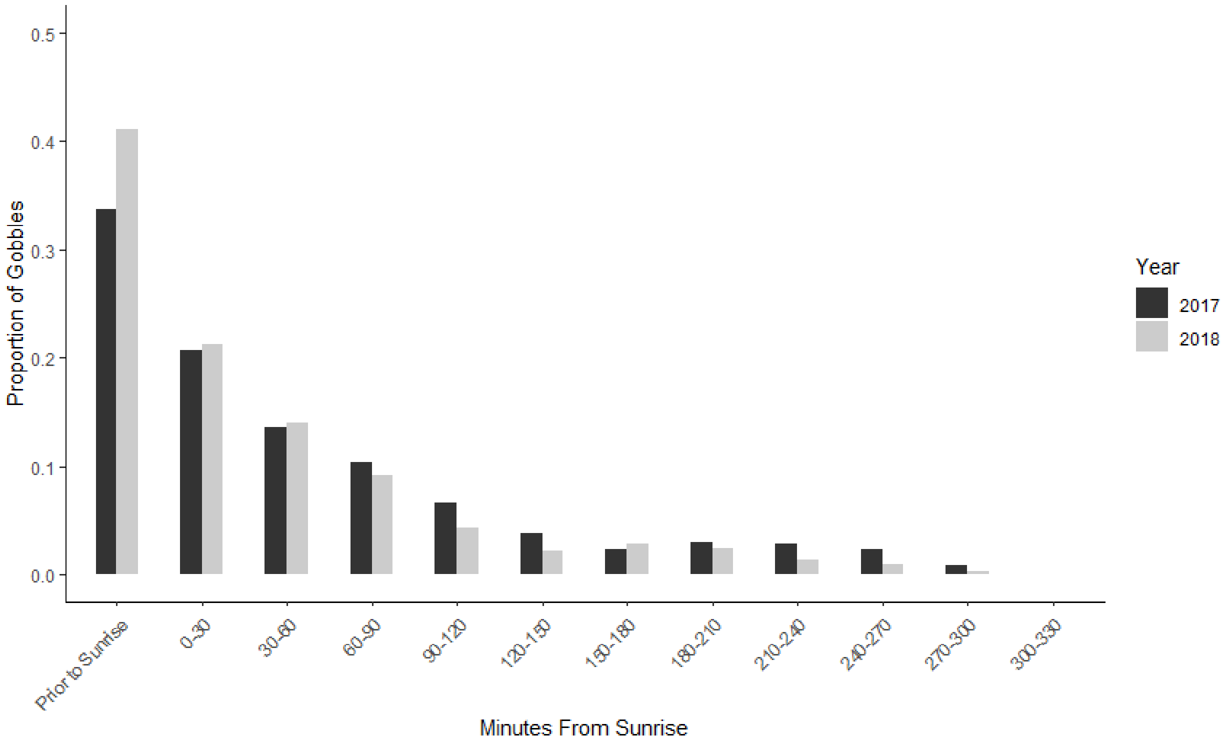

Figure 2.1: Proportion of gobbles by male Eastern wild turkeys (*Meleagris gallopavo silvestris*) recorded by 30 minutes intervals from before sunrise to 330 minutes post sunrise on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA during 2017 and 2018.

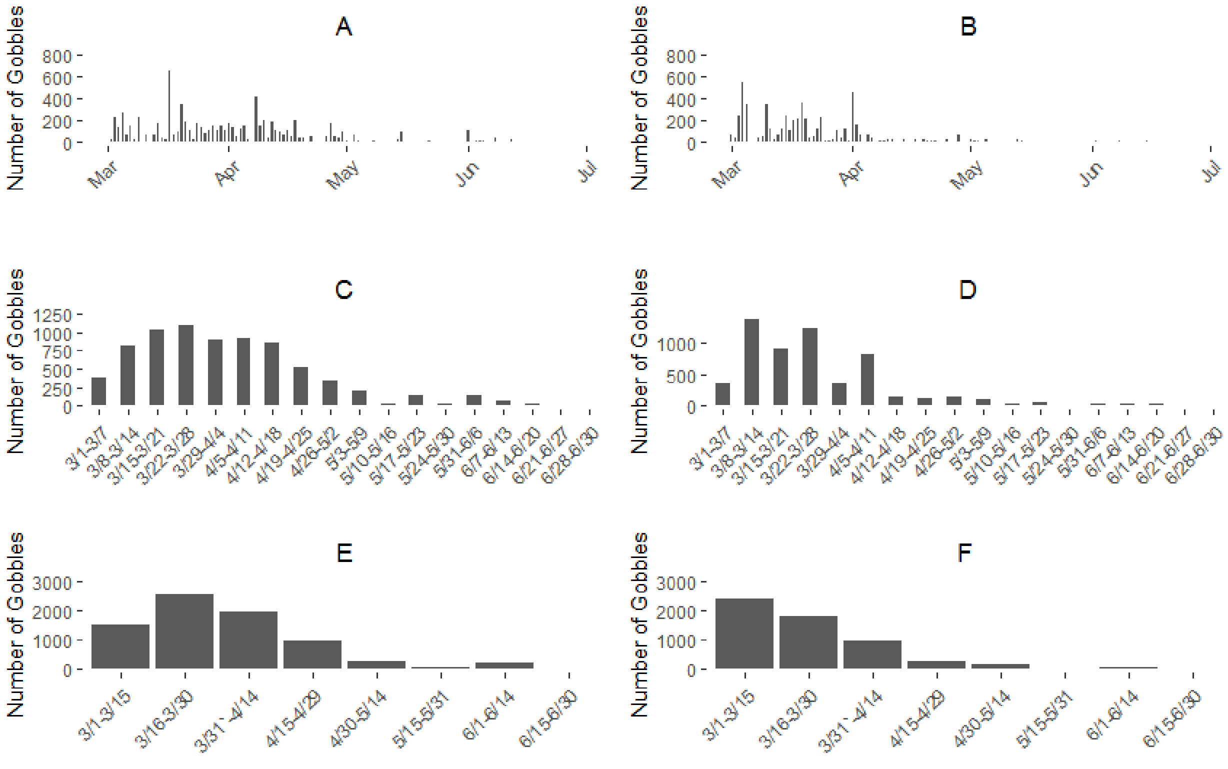

Figure 2.2: Gobbling chronology of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) aggregated daily (A for 2017 and B for 2018), weekly (C for 2017 and D for 2018), and bi-weekly (E for 2017 and F for 2018) on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA during 2017 and 2018.

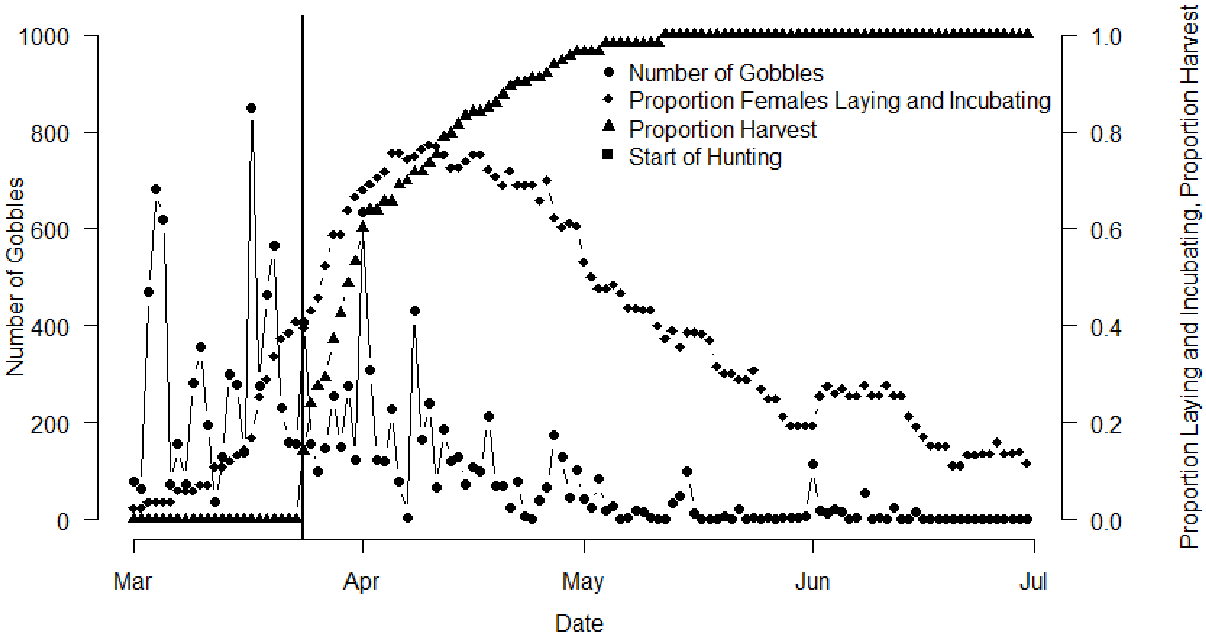

Figure 2.3: The number of daily gobbles by male Eastern wild turkeys (*Meleagris gallopavo silvestris*) relative to the proportion of GPS-marked female wild turkeys laying or incubating nests and the proportion of harvested male wild turkeys during 2017 and 2018 combined on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA.

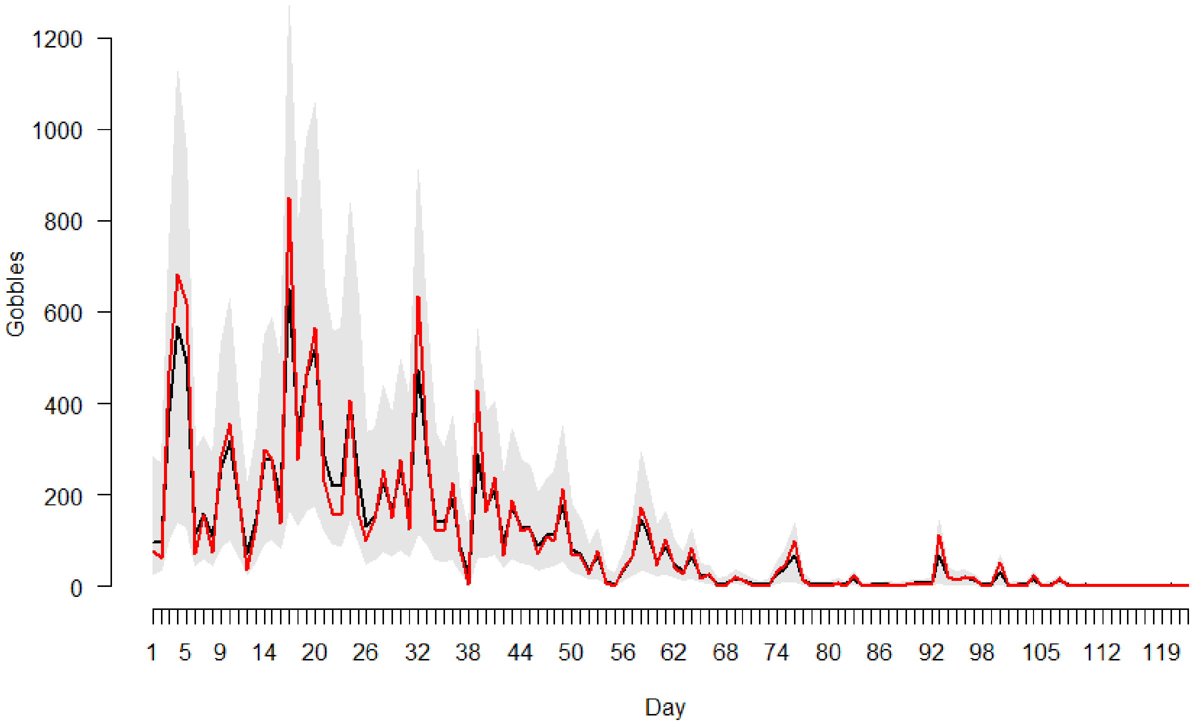

Figure 2.4: Predicted daily gobbling by male Eastern wild turkeys (*Meleagris gallopavo silvestris*) activity from results of state space model (black) with 95% confidence intervals (shaded grey) compared to observed daily gobbling activity (red) on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA.

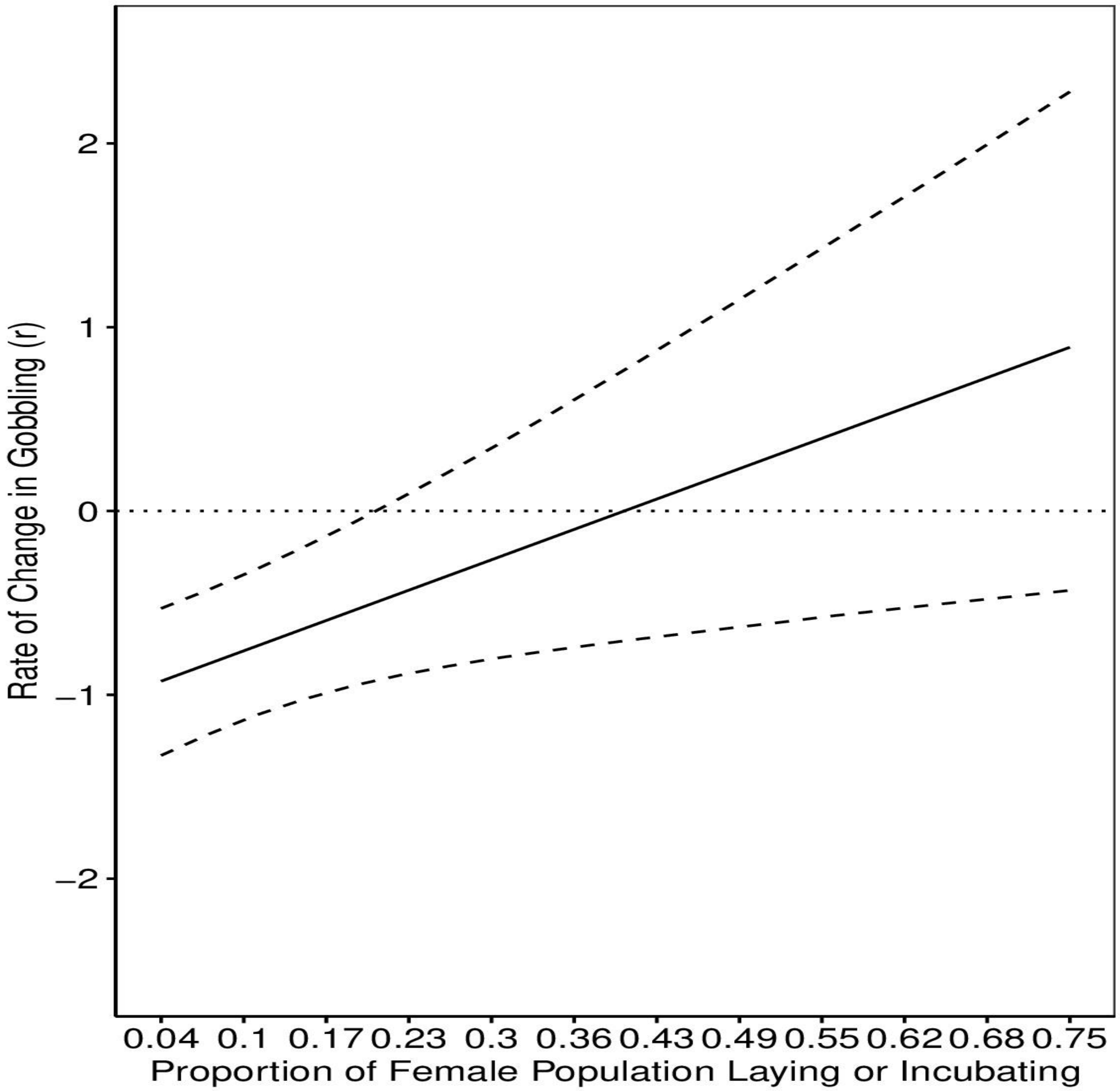

Figure 2.5: The predicted rate of change in gobbling activity of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) relative to the proportion of GPS-marked female wild turkeys in reproduction (laying or incubating a nest) prior to the start of hunting season on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA.

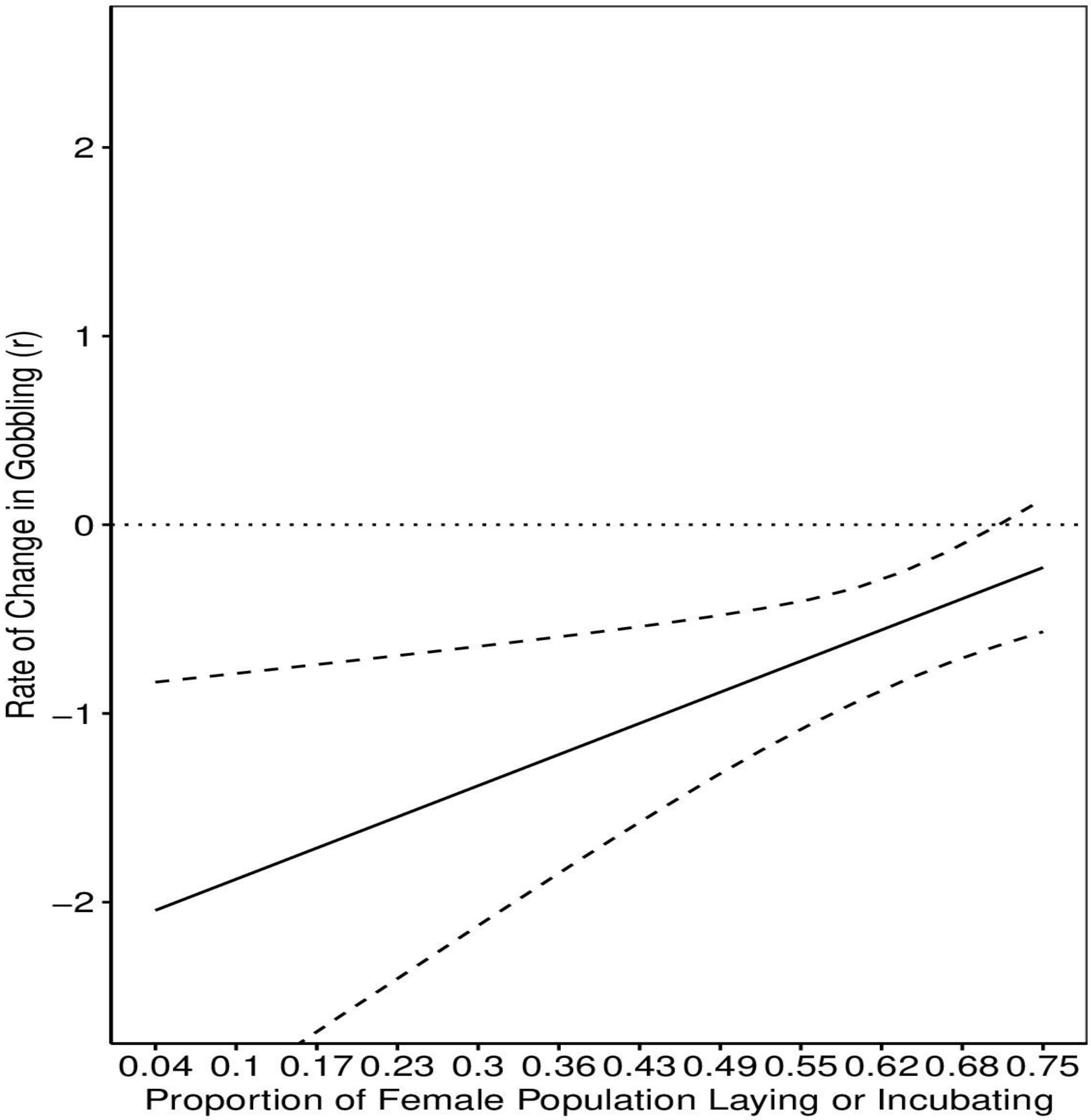

Figure 2.6: The predicted rate of change in gobbling activity of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) relative to the proportion of GPS-marked female wild turkeys in reproduction (laying or incubating a nest) after the onset of hunting season on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA.

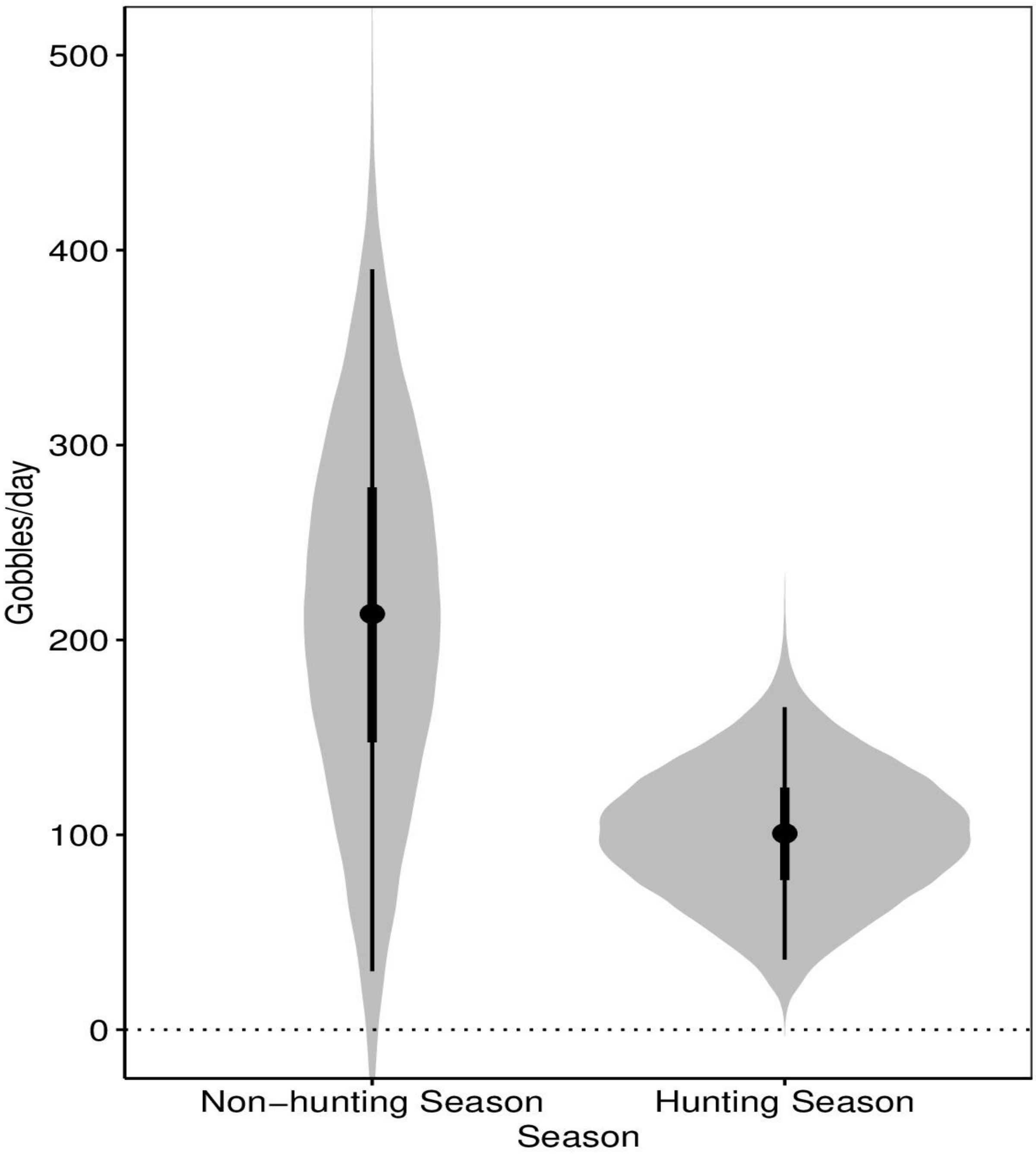

Figure 2.7: Predicted daily gobbling activity of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) with 50% and 95% quantiles before and during hunting season during 2017-2018 on B. F. Grant Wildlife Management Area and Cedar Creek Wildlife Management Area, Georgia, USA.

CHAPTER 3

INFLUENCES OF LANDSCAPE COMPOSITION AND HUNTING ON ROOST SITE USE OF MALE WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*) [2]

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[2] Wakefield, C. T., P. H. Wightman, J. A. Martin, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. To be submitted to Journal of Wildlife Management.

Abstract

The acoustic adaptation hypothesis suggests that birds may locate themselves in areas to maximize transmission of acoustic signals, such as calls, through the landscape. The primary signal used by male Eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter male turkey) during the reproductive season is the gobble, a call used to attract females and increase mating opportunities. Although habitat selection is known to influence signaling in many species, links between potential influences of habitat on signaling by male turkeys are unclear. Likewise, spring hunting of male turkeys occurs during the reproductive season, and hunting activity could influence male behaviors and calling. Because most gobbling activity occurs while male turkeys are on or close to roost sites, we evaluated roost site selection and fidelity relative to habitat and the presence of hunting activity. Prior to the onset of hunting, males roosted in hardwood and pine habitats in greater proportion than availability and roost site fidelity was low as indicated by high roost index (0.76, SD = 0.15) and large inter-roost distances (914.10 m, SD = 295.40), presumably to increase exposure to available females. After the onset of hunting season, males shifted selection to avoid pine forests and selected mixed forests but fidelity remained constant, suggesting that males may have altered selection to mitigate risk from hunting while maintaining roosting strategies. We postulate that prior to onset of hunting, males likely selected roost sites in pine stands that allowed increased propagation of calls across the landscape, but adopted alternative strategies once hunting began to avoid perceived or real predation risk.

Introduction

In polygamous mating systems, males commonly rely on signaling to display relative fitness, attract mates, and repel other males from territories (Emlen and Oring 1977). Although signals can increase mate acquisition and breeding opportunities, signaling can be costly in terms of predation risk (Berglund 1993, Stewart et al. 2005, Zanette et al. 2006). Signals involving elaborate displays or loud vocalizations may attract predators (Magnhagen 1991, Catchpole and Slater 1995, Zuk and Kolluru 1998), so individuals must balance both spatial and temporal distribution of signaling to maximize mating potential and minimize predation risk (Gintis et al. 2001, Hooper and Miller 2008). For bird species, balance may mean optimizing when to call within the reproductive season (Brunton and Li 2006, Ono et al. 2009) or a single day (Henwood and Fabrick 1979, Schmidt and Belinsky 2013), and/or optimizing the location from where they call (Henwood and Fabrick 1979, Campos et al. 2009, Ey and Fischer 2009).

According to the Acoustic Adaptation Hypothesis (AAH), habitat characteristics affect sound transmission and influence various aspects of calling behaviors (Ey and Fischer 2009). The AAH suggests that to maximize number of potential mates reached by a call, individuals should select and call from areas that allow the greatest propagation of sound across the landscape or adjust calling rates (Boncoraglio and Saino 2007, Ey and Fischer 2009). For instance, open areas allow signalers to emit fewer calls to propagate the landscape and use alternate signals (e.g., displays) compared to signalers calling in dense habitats (Koda et al. 2008, Ey and Fischer 2009, Ey et al. 2009). Thus, as habitat conditions vary temporally and spatially, males should adjust calling frequency and intensity accordingly. Furthermore, the AAH proposes individuals should select elevated areas and times with minimal background noise when calling to improve sound propagation (Parris 2002, Ey and Fischer 2009). Collectively, the AAH suggests that areas where males select to call differ in vegetative condition and acoustic properties; hence males should be selective of locations used for signaling.

In wild turkeys (*Meleagris gallopavo*), males engage in several forms of signaling to attract females (Buchholz 1995), the most common are displays and vocalizations (Miller et al.

1997a, Krakauer 2008). Gobbling is the most prominent signal used by male turkeys, and is a loud vocalization that presumably conveys fitness potential to females and hierarchical dominance to other males (Bevill Jr 1973, Miller et al. 1997b, Healy and Powell 1999, Weir et al. 2011). Gobbling activity across the reproductive season is highly variable (Chamberlain et al. 2018, Wightman et al. 2019), and seems most influenced by female receptivity (Scott and Boeker 1972, Bevill Jr 1973, Norman et al. 2001, Chamberlain et al. 2018), and hunting activity (Kienzler et al. 1995, Lehman et al. 2005, Wightman et al. 2019). Daily gobbling activity is focused at or immediately following sunrise while males are perched on or located close to their nighttime roost (Bevill Jr 1973, Hoffman 1990, Wightman et al. 2019). After gobbling at or near their roost, males tend to use the landscape to maximize exposure to available females (Little and Varland 1981, Holdstock et al. 2005), which decreases site fidelity (Hoffman 1991, Byrne et al. 2015). As a result of increased male movements during the reproductive season, distance between consecutive roost sites increases and roost site fidelity decreases (Byrne et al. 2015).

During the reproductive season, males presumably roost in areas that increase opportunities to encounter females, while balancing predation risk and potential for disturbance (Schmidt and Belinsky 2013). Therefore, optimally choosing roost locations is an important influence on relative fitness of individual males, so males should select areas to increase the likelihood of encountering receptive females. Our objectives were to evaluate male roost site selection and fidelity to observe the impacts of habitat on male gobbling activity, and examine changes in roost site selection and fidelity prior to and after the onset of hunting season. We hypothesized that males would select roost sites that optimize sound attenuation prior to hunting and exhibit low fidelity during the reproductive season. Conversely, we hypothesized that males would alter selection and fidelity in response to elevated predation risk from hunting. We predicted males would select roost sites primarily in pine and hardwood areas with low vegetation densities, and once hunting begins, avoid areas near roads and public lands. We predicted that roost site fidelity would be low throughout the reproductive period, but decrease with the onset of hunting season.

Study Area

We conducted research on B. F. Grant and Cedar Creek Wildlife Management Areas (WMA) (Figure 3.1) and surrounding privately owned areas in the Piedmont region of Georgia. B. F. Grant WMA was located in Putnam County, Georgia, USA, approximately 8 miles northwest of Eatonton, Georgia. This 4,613-ha area was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and managed cooperatively with the Georgia Department of Natural Resources, Wildlife Resources Division (GADNR). B. F. Grant WMA was bisected by Big Indian Creek and the western boundary was formed by Little River. The property was comprised of managed forest and agricultural land for livestock. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted in rye grass (*Lolium* sp.). Forested areas consisted of loblolly pine (*Pinus taeda*) forests, mixed hardwood and pine forests, and hardwood lowlands containing white oak (*Quercus alba*), sweet gum (*Liquidambar styraciflua*), yellow poplar (*Liriodendron tulipifera*), hickory (*Carya* sp.), and other oak species (*Quercus* sp.). The understory was dominated by sweet gum, eastern redbud (*Cercis canadensis*), muscadine (*Vitis rotundifolia*,), flowering dogwoods (*Cornus florida*), and briars (*Rubus* sp.). Forest management was primarily through patch cuts, thinning, and prescribed fire. The areas surrounding the property were predominately mixtures of pine forests and agricultural fields for livestock.

Cedar Creek WMA was located in Putnam County, Georgia, USA, approximately 10 miles southwest of Eatonton, Georgia. This area was owned by the U. S. Forest Service (USFS) and managed in partnership between the USFS and GADNR. Cedar Creek WMA was bisected by Big Cedar Creek and Murder Creek, and also contained portions of Glady Creek, Cedar Creek, and Badger Creek. The site was composed of managed loblolly pine forests, mixed hardwood and pine forests, hardwood valleys containing mostly white oak, sweet gum, yellow poplar, hickory (*Cary* sp.), and other oak species, and small openings for wildlife. The understory composition was similar to that on B. F. Grant WMA. The forests of Cedar Creek WMA were primarily managed through thinning and periodic (3- or 4-year return interval) dormant season fire (January through March). The land cover composition of B. F. Grant and Cedar Creek WMAs was 39.5% hardwood forests, 32.1% pine forests, 5.4% mixed forests, 19.8% open areas, 0.1% water, and 3.1% developed areas. Areas surrounding the property were predominately mixtures of pine forest and agricultural fields for livestock.

Both sites had annual spring turkey hunting seasons. The season on B. F. Grant WMA consisted of 3 hunting segments, which included an adult-child hunt from 25 March -2 April of 2017 and 24 March -1 April of 2018, an 80-person quota hunt from 3 April -9 April of 2017 and 2 April -8 April of 2018, and a general (open to the public) hunt from 10 April -15 May of 2017 and 9 April -15 May 15 of 2018. On Cedar Creek WMA, the season was a general (open to the public) hunt which opened on 25 March in 2017 and 24 March in 2018, and closed on 15 May of both years. The annual bag limit for both sites was 3 males/hunter.

Methods

Capture, Tagging, and Monitoring

We captured male turkeys using rocket nets (Delahunt et al. 2010) baited with whole kernel corn during January-March 2017 and 2018. For each turkey, we determined sex, age based on barring of the ninth and tenth primaries (Pelham and Dickson (1992), and banded individuals with uniquely numbered aluminum rivet style leg bands. We radio-tagged adult and juvenile males with a backpack-style GPS transmitter (Guthrie et al. 2011) equipped with a VHF beacon and mortality sensor weighing approximately 88 g (Lotek Wireless Inc., Newmarket, Ontario, Canada). We programmed GPS units to record locations hourly from 0500 through 2000 and one roost location at 2359 for the life of the units (Cohen et al. 2018). We released all turkeys on site immediately after processing. We then used a hand-held, 3-element Yagi antenna and R2000 or R4000 receiver (Advanced Telemetry Systems, Inc., Isanti, MN) to locate and monitor status of radio-marked individuals ≥1 time per week.

Sampling Period

We used spatial data from 1 March to 17 April to evaluate metrics of roost site selection and fidelity. We used 1 March as a start date so that we could monitor space use and roost selection when gobbling activity is known to increase during early portions of the reproductive period (Wightman et al. 2019). Likewise, we used 17 April as an end date because gobbling activity essentially ceased on our study sites by this date (Wakefield 2019). Using these start and end dates also allowed us to analyze habitat and roost selection by males within 2 comparable temporal periods prior to and after the onset of hunting.

Roost Site Selection

Most gobbling activity occurs while males are at or near roost sites (Hoffman 1991, Wightman et al. 2019), so we evaluated roost site selection with a distance-based analysis to determine the relative influence of habitat on sites chosen by males for roosting. We constructed 99% utilization distributions (UD) using dynamic Brownian Bridge Movement Models for each male using all GPS locations (day and night, (Kranstauber et al. 2012, Byrne et al. 2014), and generated 5 matched random locations for each roost site within each UD. We considered random locations as available roost sites, and compared them to used roost sites as a measure of habitat selection. We used the National Land Cover Database (NLCD; 2011) and Normalized Difference Vegetation Index (NDVI; 2017, 2018) to examine habitat characteristics at each roost and random location. We relied on NLCD data to assess roost selection relative to land cover types (Homer et al. 2015), and NDVI data as a proxy for vegetation density (Pettorelli et al. 2005). We reclassified NLCD data into 6 habitat types we believed would be relevant to roost site selection, which included hardwood (combination of deciduous forest and woody wetlands), pine (evergreen forest), mixed forest, open areas (combination of barren land, shrub/scrub, grassland/herbaceous, pasture/hay, and cultivated crops), developed (developed areas at all intensities), and open water (Hurst et al. 1991, Chamberlain et al. 2000, Byrne et al. 2015). In addition to landcover types and vegetation density, we believed roads/trails and private property could also be important factors influencing male roost site selection. Linear openings associated with roads can function as displaying areas (DeYoung and Priebe 1987), but also a source of increased disturbance and human activity (McDougal et al. 1990, Erxleben et al. 2011). We postulated that private lands were areas of reduced predation risk with reduced disturbance during hunting season relative to public lands. We used ArcMap 10.3 (Environmental Systems

Research Institute, Inc., Redlands, California) to convert habitat attributes to rasters where each pixel contained a measurement of the distance to each attribute. We then used the Euclidean distance tool in ArcMap to measure distance to each attribute from each roost and random location. We buffered all location by 250 meters and extracted the average NDVI value at for each location to measure vegetation density.

We modeled male roost site selection prior to and during hunting using a conditional logistic regression model in the rstanarm package in program R (R Core Team, 2018). Conditional logistic regression models allowed us to quantify the effect of habitat variables on roost site selection using matched selected and random locations, and account for individual heterogeneity in roost site selection. We scaled all distance variables by a factor of 100 m to ensure model convergence. We scaled NDVI values using the scale function in program R, which subtracted the mean from each value and divided by 1 standard deviation, and then extracted NDVI values at all locations.

Roost Site Fidelity

Previous authors have noted that male turkeys may decrease roost site fidelity during the reproductive season, presumably to maximize encounters with receptive females (Hoffman 1991, Byrne et al. 2015). We used methods outlined by Byrne et al. (2015) to assess roost site fidelity by developing a roost index (RI) to quantify reuse of roosts prior to and after the onset of hunting. We calculated RI as the number of individual roost sites used prior to and after the onset of hunting divided by number of nights within the period. We determined number of individual roost sites by buffering each roost location by 20 m, the estimated GPS error (Guthrie et al. 2011), and counting the number of locations; we considered buffers that overlapped as a single roost location. We determined number of unique roost sites and divided by the total number of nights prior to and after the onset of hunting to determine the roost index (RI, (Byrne et al. 2015). A RI value of 1 would indicate that an individual exhibited no fidelity and roosted at a different site each night, whereas values approaching 0 indicated strong fidelity to few roost sites. We calculated the straight-line distance (m) between consecutive roost sites as an additional measure of roost site fidelity. We then calculated the average daily distance between consecutive roost sites for each male prior to and after the onset of hunting. We used 2 sample *t*-tests ($\alpha = 0.05$) to test potential influences of hunting on RI and inter-roost site distances to evaluate roost site fidelity. All statistical analyses were performed using R (R Core Team, 2018).

Results

We captured and radio-marked 33 males (14 in 2017; 17 in 2018), and collected sufficient data on 29 males for analysis. Size of 99% UDs ranged from 132.39 ha to 1310.67 ha before hunting season and 122.04 ha to 1147.68 ha during hunting season. We observed that 22 of the 29 males used in analyses were still alive on April 17.

Prior to hunting season, male turkeys selected roosts in hardwood forest ($\beta = -0.845$, 95% CI = -1.114, -0.586), followed by pine forest ($\beta = -0.235$, 95% CI = -0.414, -0.060; Table 3.1; Figure 3.2). Vegetation density did not influence roost site selection prior to (NDVI $\beta = -0.129$, 95% CI = -0.475, 0.226) or after the onset of hunting (β NDVI = -0.074, 95% CI = -0.398, 0.224). Prior to hunting season, males did not select or avoid mixed forest, open areas, development, water, private property, and roads (Table 3.2; Figure 3.2). After the onset of hunting, males weakly selected for mixed forest (β Mixed Forest:Hunt = -0.161, 95% CI = -0.300, -0.035; Figure 3.2), but avoided pine forest (β Pine = 0.276, 95% CI = 0.033, 0.501;

Figure 3.2). During hunting season, males did not select or avoid hardwood forest, open areas, development, water, private property, and roads (Table 3.2; Figure 3.2)

We observed mean RI of 0.78 (SD = 0.15) for the entire study period (March 1 to April 17 of 2017 and 2018), and RI varied greatly across individuals. We noted that some males showed no fidelity to roost sites (RI = 1.0) whereas others did (RI = 0.17). The RI was similar (t = -1.05, df = 47, P = 0.30) before (0.76) and after (0.80) onset of hunting (Figure 3.4). Distances between consecutive roost sites averaged 870.48 m (SD = 769.75, Figure 3.3), and varied from 0 m (≤20 m, the error of the GPS units) to 4644.87 m. Additionally, distances between consecutive roost sites did not differ before (914.10 m) and after (811.81 m) onset of hunting (t = 1.31, df = 50, P = 0.20).

Discussion

Male wild turkeys must balance the spatiotemporal aspects of their signaling to maximize breeding opportunities and minimize predation risk. The AAH theorizes that one way to maximize breeding opportunities is to vocalize in the best acoustic environments, where calls attenuation or deterioration across the landscape is reduced. Most gobbling activity occurs while male turkeys are roosting (Hoffman 1990, Wightman et al. 2019), hence we evaluated habitat selection for and fidelity to roost sites under the assumption that these sites were used for calling and sound propagation. We found that male turkeys primarily roosted in hardwood and pine forests prior to onset of hunting, but shifted selection once hunting began. Likewise, we noted that males on average showed little fidelity to roost sites and moved considerable distances between consecutive roosts. Collectively, our findings do not support assertions of the AAH, and suggest that hunting activity may prompt males to alter habitats chosen for roosting.

Males selected hardwood and pine areas for roosting prior to onset of hunting, presumably roosting in these areas to maximize propagation of calls and limit sound degradation and obstruction (Brown et al. 1995, Couldridge and Van Staaden 2004, Nicholls and Goldizen 2006), while also maximizing exposure to females known to select these same habitats for roosts (Miller et al. 1999, Chamberlain et al. 2000). Female turkeys often select hardwood and pine habitats for roosting, but have shown strong selection for pine forests in comparable landscapes with onset of the reproductive season (Miller et al. 1999, Chamberlain et al. 2000, Miller and Conner 2007). Open areas can be important to turkeys for displaying on some landscapes (Barwick and Speake 1973, Godwin et al. 1992, Holdstock et al. 2005), but our analyses were focused solely on roost sites, which would be associated with forested areas rather than more open landscapes. Previous authors have noted that females often selected roost sites associated with water (Burk et al. 1990a, Chamberlain et al. 2000), likely because open water has acoustic properties and better sound transmission for calling (Parris 2002). We note that open water was scarce on our study sites, and habitats classified as water tended to be ponds, rather than areas likely to attenuate sound. Likewise, habitats classified as water only constituted <1% of available habitats on our study site.

We observed high RI values, suggesting low reuse of roost sites, consistent with the findings of Byrne et al. (2015). Males also tended to move relatively great distances between roost sites, suggesting that calling from a particular roost site and then shifting to other roosts may be a strategy used by male Eastern turkeys during the reproductive season. Additionally, male roost site fidelity was unaffected by the presence of hunting activity, suggesting decreased fidelity may also alleviate risk associated with consecutively calling from the same location. High RI values, combined with considerable distances between consecutive roost sites, suggests that males do not typically select the same roost sites across consecutive nights. Low roost site fidelity may occur because males are known to use the greatest area and travel most during the reproductive season (Hoffman 1991, Godwin et al. 1994, Holdstock et al. 2005), presumably to increase opportunities to maximize sound propagation across the landscape by calling from new locations and maximize probability of contacting available females (Hoffman 1991, Byrne et al. 2015, Gross et al. 2015b). Additionally, low roost site fidelity suggests that optimal trees for roosting and calling are not a limited resource for Eastern wild turkeys on landscapes similar to those detailed herein (Byrne et al. 2015). Future research should explore the possibility that males shift roosting locations to increase exposure to new females and increase breeding opportunities, while also reducing increases in predation risk associated with consistent vocalization in a given area (Boyko et al. 2004).

Hunting activity has been shown to influence male space use, movements, and calling (Kienzler et al. 1995, Lehman et al. 2005, Wightman et al. 2019). We found that males avoided pines after the onset of hunting season. Superficially, selection against pine after the onset of hunting season could simply point to a seasonal shift away from pine habitat (Godwin et al. 1992), but previous authors have noted a strong selection of pine habitats by females as reproduction began (Burk et al. 1990b, Smith et al. 1990, Thogmartin 1999, Chamberlain et al. 2000). Hence, we would expect males to select roosts in or near these same habitats to increase exposure to females (Miller et al. 2000), particularly as competition amongst males increases prior to laying and incubation (Godwin et al. 1994, Badyaev and Faust 1995, Badyaev et al. 1996, Chamberlain et al. 2018). Therefore, we postulate that avoidance of pines after hunting began was more likely related to increases in human activity in pine habitats during hunting season, prompting males to avoid roosting in pine habitats to mediate perceived or real predation risk.

Prior to onset of hunting, male turkeys presumably selected roost sites that allowed the greatest propagation of calls across the landscape (Erdtmann and Lima 2013) while maximizing the probability that a call would attract available females (Parris 2002), which would lend support to the AAH. Conversely, our findings suggest that after hunting began, males avoided pine stands that likely afforded preferred roost sites with appropriate sound propagation, likely to alleviate predation risk associated with hunting activity. Notably, contemporary literature has clearly demonstrated that gobbling activity declines (Chamberlain et al. 2018, Wightman et al. 2019) and may cease (this study) in the presence of hunting. Therefore, we postulate that shifts in roost site selection coupled with low roost site fidelity after the onset of hunting activity are to mediate for real or perceived predation risk (Laundré et al. 2010, Ciuti et al. 2012, Coleman and Hill 2014).

Management Implications

Male wild turkeys are hunted primarily during the reproductive season, but the full effect of hunting on male reproductive behaviors are not known. Hunting activity can negatively influence gobbling activity, but effects of hunting on roost site selection by males has been poorly documented. Our findings suggest that in response to increased predation risk through hunting activity, males alter selection of roosts and by default, locations from which they call prior to and immediately after sunrise. Agencies should consider how hunting can alter behaviors, including gobbling activity and roost site selection and fidelity, and how changes in behaviors could negatively influence reproduction. Future research should evaluate potential consequences of roost site selection prior to and after onset of hunting on metrics of individual fitness, such as survival and susceptibility to harvest.

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Table 3.1: Average distance (m) to habitat variables and average vegetation density (NDVI) within in a 250 meter buffer around roost and random locations for male Eastern wild turkeys (*Meleagris gallopavo silvestris*) prior to and during hunting season on Cedar Creek Wildlife Management Area and B. F. Grant Wildlife Management Area Georgia, USA, from 1 March to 17 April of 2017-2018.

Habitat Attributes	Roost Prior to Hunting	Roost During Hunting	Random Prior to Hunting	Random During Hunting
NDVI	0.42±0.033	0.42±0.034	0.42±0.033	0.42±0.034
Hardwood	29.18±50.13	25.81±47.76	46.6±60.51	44.17±56.68
Pine	65.11±67.030	72.22±77.43	67.09±78.66	61.88±79.18
Mix	197.08±166.27	166.96±145.94	194.45±172.83	181.23±156.31
Open	115.38±95.53	124.54±99.34	109.72±113.70	134.18±126.58
Developed	509.87±333.94	512.69±359.18	469.43±335.73	468.49±337.64
Water	1460.81±988.82	1381.45±992.51	1436.65±1023.56	1400.5±998.45
Private	363.48±492.35	365.40±492.58	365.44±484.61	353.62±459.11
Road	251.16±217.50	303.96±244.81	225.13±202.96	263.37±240.21

Table 3.2: Estimated effects of habitat variables from a conditional logistic regression model of roost site selection of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) measured as distance to each attribute (scaled by 100 m) and how selection for each habitat attribute changed after the onset of hunting season on Cedar Creek Wildlife Management Area and B. F. Grant Wildlife Management Area Georgia, USA, from 1 March to 17 April of 2017-2018.

Habitat Variables	Average Beta Coefficient	Standard Deviation	Quantiles				
			2.50%	25%	50%	75%	97.50%
NDVI	-0.129	0.18	-0.475	-0.254	-0.127	-0.007	0.226
Hardwoods	-0.845	0.135	-1.114	-0.935	-0.842	-0.751	-0.586
Pine	-0.235	0.092	-0.414	-0.297	-0.235	-0.173	-0.06
Mixed Forest	0.043	0.048	-0.05	0.011	0.043	0.075	0.14
Open Areas	0.02	0.062	-0.101	-0.021	0.020	0.062	0.137
Development	0.039	0.027	-0.016	0.021	0.039	0.056	0.092
Water	0.022	0.016	-0.009	0.011	0.023	0.034	0.054
Private	-0.002	0.031	-0.065	-0.022	-0.001	0.019	0.056
Road	0.058	0.037	-0.011	0.032	0.058	0.083	0.13
Hunt	0.506	0.295	-0.071	0.309	0.504	0.706	1.091
NDVI:Hunt	-0.074	0.16	-0.398	-0.181	-0.073	0.035	0.224
Hardwoods:Hunt	-0.113	0.182	-0.453	-0.24	-0.114	0.011	0.233
Pine:Hunt	0.276	0.121	0.033	0.195	0.278	0.362	0.501
Mixed Forest:Hunt	-0.161	0.068	-0.30	-0.204	-0.158	-0.115	-0.035
Open Areas:Hunt	-0.079	0.074	-0.223	-0.129	-0.078	-0.031	0.061
Development:Hunt	-0.016	0.034	-0.087	-0.038	-0.015	0.007	0.047
Water:Hunt	-0.033	0.020	-0.073	-0.045	-0.032	-0.02	0.004
Private:Hunt	-0.016	0.036	-0.091	-0.039	-0.014	0.007	0.050
Road:Hunt	0.014	0.048	-0.084	-0.017	0.014	0.045	0.105

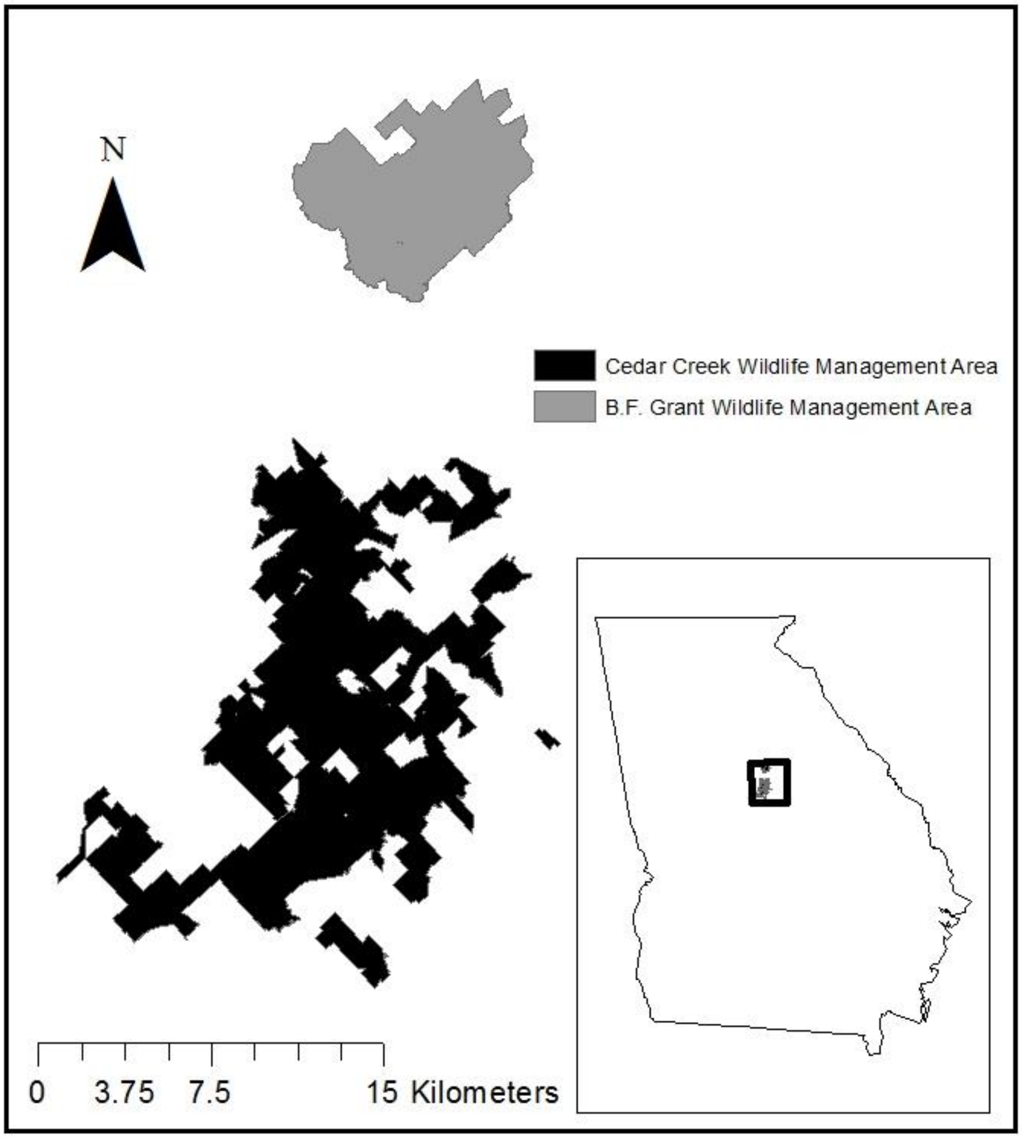

Figure 3.1: B.F. Grant and Cedar Creek Wildlife Management Areas in Georgia, USA.

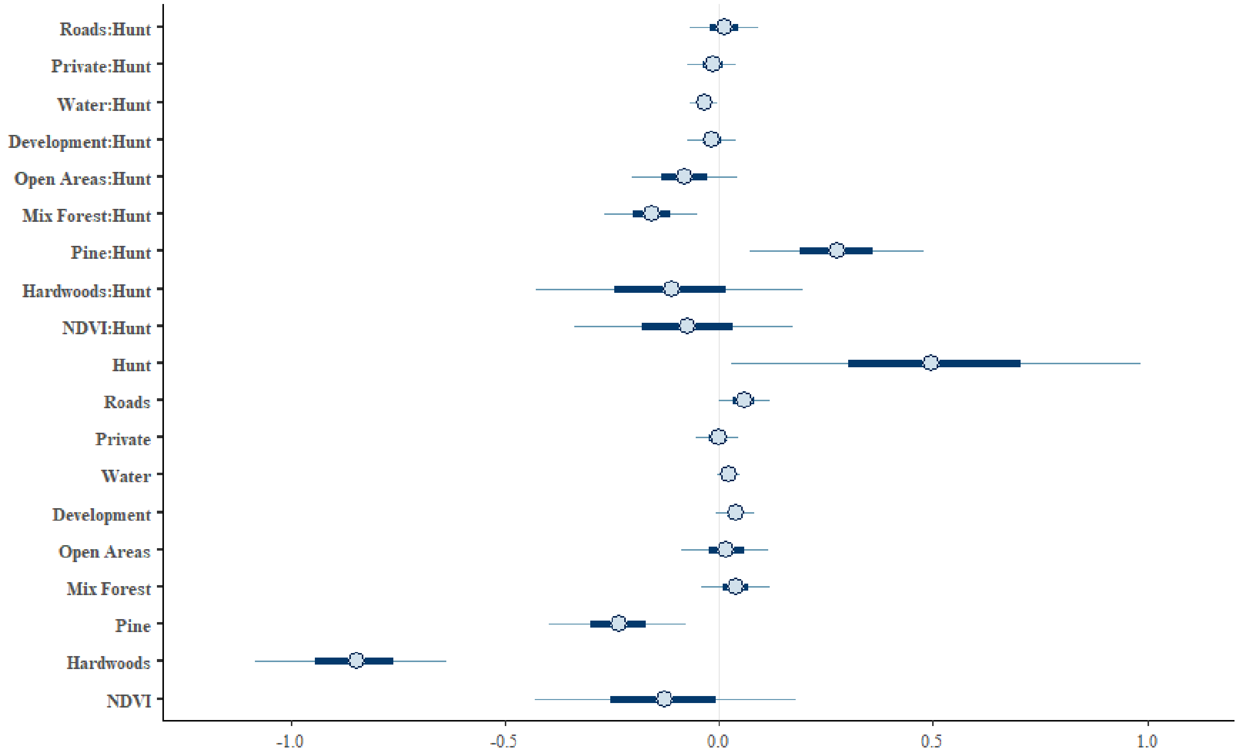

Figure 3.2: Estimated effects of habitat attributes (NDVI, scaled by subracting the mean and dividing by 1 standard deviation), and landcover types (hardwoods, pine, mixed forest, open area, developed areas, water, private property, and roads) with 50% (thick line) and 95% (thin line) crediblilty intervals measured as distance to each attribute (scaled by 100 m) from a conditional logistic regression model on roost site selection of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) prior to and after the onset of hunting (indicated by :Hunt) season, on Cedar Creek and B. F. Grant Wildlife Management Areas, Georgia, USA during1 March to 17 April of 2017-2018.

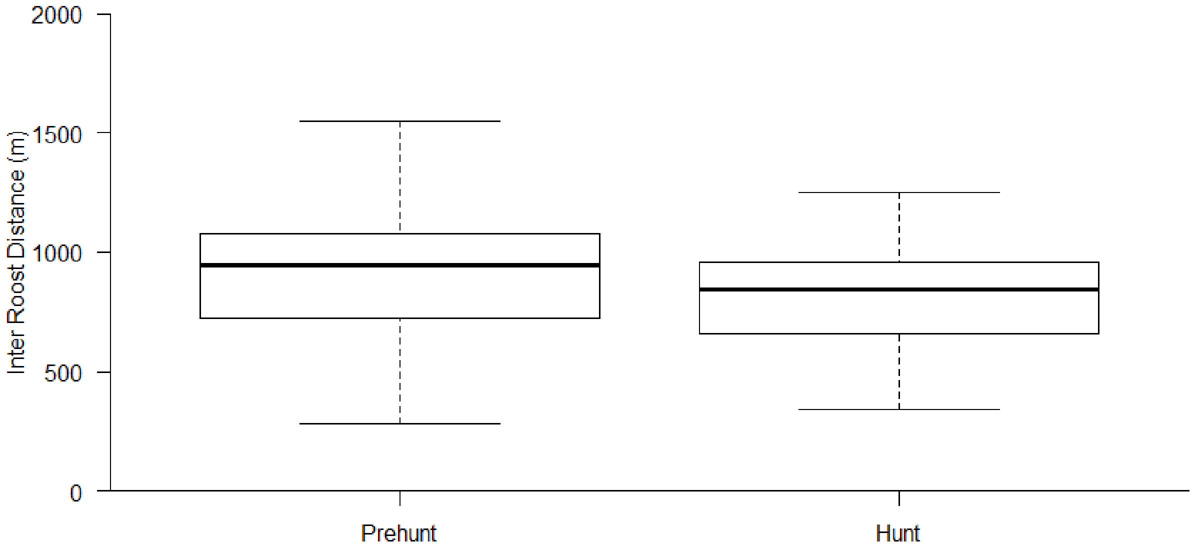

Figure 3.3: Average distance between consecutive roost sites of male Eastern wild turkeys (*Meleagris gallopavo silvestris*) prior to (prehunt) and after the onset of (hunt) hunting season on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, during1 March to 17 April of 2017-2018.

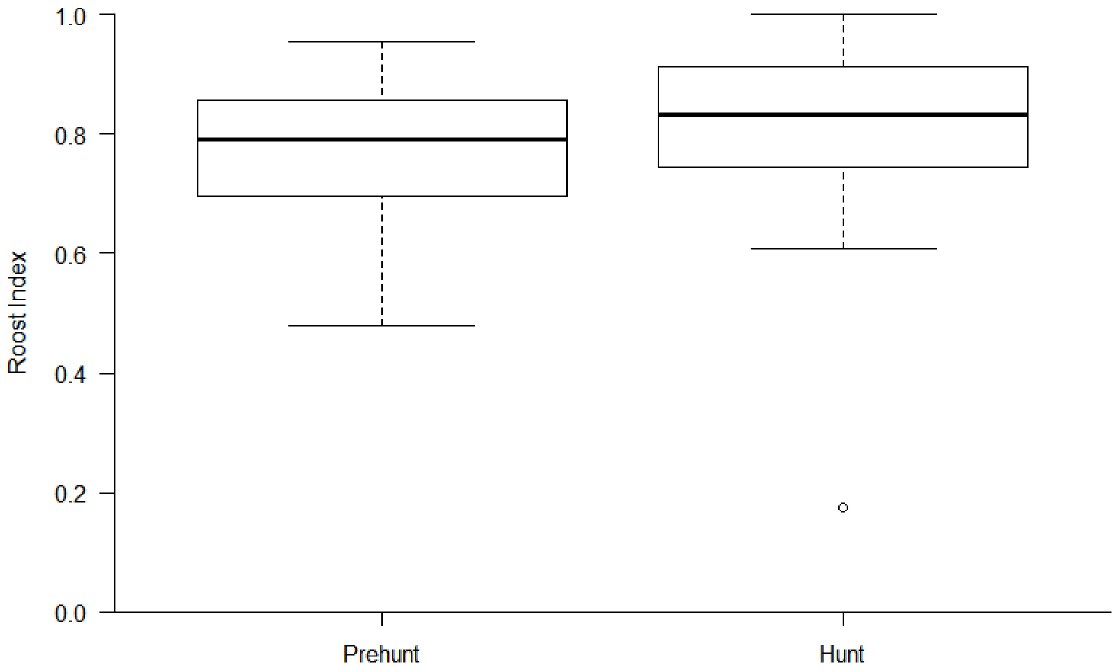

Figure 3.4: Roost index, a measure of roost site fidelity, for male Eastern wild turkeys (*Meleagris gallopavo silvestris*) before (prehunt) and during (hunt) hunting season on B. F. Grant and Cedar Creek Wildlife Management Areas, Georgia, USA, during 1 March to 17 April of 2017-2018.

CHAPTER 4

CONCLUSIONS

Wild turkeys (*Meleagris gallopavo*) use a polygynous mating system where males engage in multiple courtship behaviors, including displaying and vocalizations (gobbling) to attract females. The primary factor believed to influence gobbling by male wild turkeys is female reproductive behaviors, but hunting activity has been shown to negatively influence gobbling activity. The magnitude of effect of female reproduction and hunting activity on daily gobbling activity has not previously been documented. Likewise, most gobbling activity occurs while male turkeys are on or close to roost sites, so roost site selection and fidelity can be used to examine the relationship between habitat and calling in male turkeys. Lastly, roost site selection, and hence calling by male wild turkeys, could be influenced by habitat conditions and hunting activity that vary temporarily, seasonally, and daily, but these influences have not been well documented in wild turkeys. My study provided new information on the magnitude of effect that hunting activity and female reproductive behaviors have on daily gobbling activity. I also detailed roost site selection and fidelity by males relative to habitats and the presence of hunting.

I used autonomous recording units and GPS transmitters to monitor gobbling activity by male turkeys and reproductive behaviors of female turkeys in the Piedmont region of Georgia, USA, during 2017-2018. I noted that ~60% of gobbling activity occurred within 1 hour of sunrise. I observed a weak negative relationship between daily gobbling activity and gobbling activity the following day. As the reproductive season progressed gobbling activity decreased, and I observed most gobbles (~63%) occurred during March and gobbling declined markedly from April through May both years. However, I observed that as the proportion of females engaged in reproductive behaviors increased, expected daily gobbling activity increased. Conversely, I observed that hunting activity had a strong negative effect on daily gobbling activity, and the effect of hunting activity was disproportionately greater than the positive effect of female reproductive behaviors. My findings suggest that predation risk via hunting activity by humans is an important determinant of gobbling activity by males, and that this predation risk may have mediating effects on the mating system of wild turkeys.

I evaluated roost site selection and fidelity of male turkeys relative to habitat and the presence of hunting activity. Prior to onset of hunting, males roosted in hardwood and pine habitats and roost site fidelity was low, presumably to increase exposure to available females. After hunting began, males shifted selection to avoid pine forests and selected mixed forests, suggesting that males may have altered selection to mitigate risk from hunting. I observed high roost index and large inter-roost distances suggesting that roost site fidelity was low, and hunting activity had minimal impacts on roost site fidelity. I postulate that prior to onset of hunting, males likely selected roost sites in pine stands that allowed increased propagation of calls across the landscape, but adopted alternative strategies once hunting began to avoid perceived or real predation risk.

Collectively, my findings suggest that hunting may influence behaviors in wild turkeys by suppressing gobbling activity and altering roost selection during the reproductive season. These influences could create mediating effects on wild turkey reproduction by altering mate selection and the ability of males to locate in proximity to receptive females. To alleviate potential negative impacts of hunting on wild turkey reproduction, state wildlife agencies should set regulatory frameworks that ensure that hunting is timed when mate selection has already occurred, which would coincide with peaks in onset of incubation. Specific to my study sites, this recommendation would translate to adjusting hunting season opening dates from 24 March to 14 April.