FACTORS INFLUENCING THE SPACE USE OF A NONHUNTED POPULATION OF EASTERN WILD TURKEYS

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By
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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

FACTORS INFLUENCING THE SPACE USE OF A NONHUNTED POPULATION OF EASTERN WILD TURKEYS

Presented by Holly Lott
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and hereby certify, in their opinion, it is worthy of acceptance.

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me throughout my master's degree, especially for putting up with the many long days I worked during the field season.

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Factors Influencing the Space Use of a Nonhunted Population of Eastern Wild Turkeys

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Abstract

Wild turkeys (*Meleagris gallopavo)* have been an economically and culturally important game species in North America for many decades. Recent declines in abundance and productivity in several populations of wild turkeys, have caused widespread concern among researchers and managers. After near extinction in the early 1900's followed by successful restoration efforts in the late 1900's, researchers are focused on preventing populations of wild turkeys from declining again. Male wild turkeys are the only game bird in the contiguous United States hunted during their reproductive season, however, there are many aspects of male reproductive ecology that are not well understand. Because male wild turkeys use a polygynous-promiscuous mating system and do not participate in nesting or brood-rearing, wild turkey research has mostly focused on female reproductive ecology, leading to a gap in knowledge regarding male reproductive behaviors. Because hunting pressure can affect the spring behaviors of wild turkeys, it is critical to conduct research on male wild turkey reproductive behaviors in a nonhunted population. Because most populations of wild turkeys are hunted in the United States, the opportunity to study nonhunted populations is rare. In this study, I tracked the movements of 19 male eastern wild turkeys (*Meleagris gallopavo silvestris*) during the spring mating and summer non-mating seasons of 2020 and 2021 on the Savannah River Site near Aiken, South Carolina, in order to assess seasonal space use of

male wild turkeys in a nonhunted population. In addition, I looked for evidence of cooperative courtship and kin selection operating in this population. I used dynamic Brownian Bridge Movement Models to estimate daily and seasonal ranges. Median daily mating season ranges of 100% of males were larger than median daily non-mating season ranges, and 83% of males had larger mating season ranges than non-mating season ranges. Linear mixed effects models showed season to be an important predictor of both daily range size and distance between consecutive nightly roost location. Only one male exhibited temporal autocorrelation in daily range size during the mating season. While 33% of males exhibited temporal autocorrelation in the size of daily non-mating season ranges, all but one had ≤ 2 significantly autocorrelated days. Males did not exhibit observable differences between seasons in the intensity of aggregation of daily locations compared to seasonal locations, and there was significant daily variation in both seasons. The lack of temporal autocorrelation and variation in daily aggregation intensity in both seasons indicates that male wild turkeys may not use space within their seasonal ranges differently between mating and non-mating seasons. I conducted a proximity analysis and calculated relatedness of male dyads to determine if there was evidence of cooperative courtship and kin selection operating in this population. I identified six pairs of first-order relatives (full siblings or parent-offspring), three pairs which were trapped together and three which were trapped separately. While I only had GPS data for two pairs of first-order relatives, they exhibited opposite behaviors. One pair traveled together throughout the study period and one pair never traveled together, indicating that cooperative courtship via kin selection may not be an obligate behavior for wild turkeys on the Savannah River Site. Additionally, one unrelated pair stayed together throughout the

breeding season, indicating that kin selection may not be the only explanation of

cooperative courtship in this population. This research highlights the need for future

studies that focus on how courtship behaviors may differ across subspecies and habitat

types.

Chapter 1: History and Reproductive Ecology of Wild Turkeys in North America

History and Current Status of Wild Turkeys in North America

Prior to European settlement, the wild turkey (*Meleagris gallopavo*) was widespread and abundant across North America, with a native distribution encompassing 39 U.S. states and Ontario. After European colonization, wild turkeys were hunted year-round without bag limits while simultaneously, many natural landscapes were converted into agriculture, leading to population declines (Kennamer et al. 1992). By the early 1800's, wild turkeys could no longer be found in much of their original range apart from certain isolated locations in the Southeastern U.S. By 1920, wild turkeys were completely extirpated from 18 states in their historic range and populations reached their lowest levels in the 1930's (Kennamer et al. 1992, Eriksen et al. 2015).

As agricultural fields were abandoned in the 1930's and 1940's, succession of fields into trees and shrubs provided a start to turkey habitat restoration. Legislation such as the Lacey Act and the Pittman-Robertson Act further paved the way for restoration of wild turkey populations. Focused wild turkey restoration began in the 1950's when state wildlife agencies began reintroducing wild turkeys to areas in which they were extirpated. These efforts showed great success and populations started to grow rapidly. In the 1990's, the population of wild turkeys in the U.S. was approximately 3.5 million (Kennamer et al 1992) and in 2009 it was estimated at 6.5 million (Eriksen et al 2015).

Despite the wide-scale success of wild turkey restoration programs and significant growth of wild turkey populations over the last several decades, states have recently documented declining trends in wild turkey abundance and productivity indices. It is estimated wild turkey populations declined by approximately 5.96-7.52% between 2009

and 2014 (Eriksen et al. 2015). Around the same time as these perceived declines in wild turkey abundance, regional declines in productivity of eastern wild turkey (*M. g. silvestris*) populations in the Southeast (Byrne et al. 2015) and Northeast United States (Casalena et al. 2015) were observed. Because wild turkey population growth is heavily influenced by productivity (Vangilder et al. 1987, Miller et al. 1995), biologists are concerned that regional population declines and reproductive declines may be related (Byrne et al 2015, Eriksen et al. 2015). Because wild turkeys are an economically and ecologically important game species, much research has focused on gaining a better understanding of wild turkey reproductive ecology in hopes of reversing and preventing population and productivity declines.

Wild Turkey Reproductive Ecology

The social structure and reproductive behaviors of wild turkeys are complex, and many aspects are still not well understood. During winter, wild turkeys flock together usually in groups of adult males, juvenile males, or females. Flocks have strict linear dominance hierarchies and hierarchies are different between sexes and between and within same sex flocks (Watts and Stokes 1991, Healy 1992). Order of dominance in all hierarchies is determined by fighting. Since observations by Watts and Stokes (1971), it has been assumed that the structure of female winter flocks consists mostly of unrelated females while the structure of male winter flocks is made up of multiple sibling groups of male wild turkeys. When the winter flocks break up in early spring, the sibling groups of males stay together throughout the year (Watts and Stokes 1971, Healy 1992).

Male wild turkeys experience strong sexual selection as a result of female mate choice resulting in the development of dramatic courtship behaviors and sexual

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dimorphism (Pehlam and Dickson 1992, Krakauer 2008). Adult males are twice as heavy as females and have colorful iridescent plumage, spurs, and skin ornamentation that changes size and color during interactions with females (Pelham and Dickson 1992). Male turkeys use elaborate courtship displays to attract females including vocalizations (gobbling) and strutting (Healy 1992). Watts and Stokes (1971) observed that all males display to attract females, however, the dominant males are responsible for the majority of mating attempts and most other males rarely get the opportunity to mate. Wild turkeys use a polygynous-promiscuous mating system in which males do not aid females in nesting or brood-rearing, and males and females may both have multiple mates during a season (Healy 1992). Because of this lack of involvement in parental responsibilities (Watts and Stokes 1971, Healy 1992), most research on reproductive ecology has focused on females and female reproductive success. Recent female reproductive ecology research has focused on female habitat selection (Miller and Connor 2007, Pollentier et al. 2017), nest site selection and success (Lehmen et al. 2008, Byrne et al. 2013, Streich et al. 2015, Kilburg et al. 2014, Little et al. 2016, Yeldell et al, 2017, Chamberlain et al. 2018, Wood et al. 2019), and brood habitat use and survival (Spears et al 2007., McCord et al. 2019, Wood et al. 2019). There has been comparatively less attention focused on male reproductive ecology and many aspects of the complex social structure and courtship behavior of wild turkeys, of which males play an important role, are not fully understood.

Harvest Regulations and Research

Wild turkeys are the only North American game birds that are hunted during their reproductive season. Forty-nine states have spring gobbler seasons which provides many

wildlife managers with challenges in preventing disturbance to mating and nesting activities. (Isabelle et al. 2018). Additionally, hunter satisfaction is based on hearing gobbles, so managers are tasked with setting regulations that simultaneously satisfy hunters and minimize negative effects on productivity (Vangilder et al. 1990). Historically, male turkey harvest regulations have been set based on the assumption that there are two peaks in gobbling activity, the first peak coinciding with the breakup of winter flocks, and the second with the onset of nest incubation (Kurzejeski and Vangilder 1992, Miller et al. 1997). In an attempt to satisfy hunters and minimize negative effects on reproduction, managers have traditionally set season boundaries that coincide with the second peak in gobbling. Until recently, it was widely assumed that because males show no parental involvement, setting hunting seasons for males that overlap with the breeding season would have little effect on their populations or reproductive activities. It is also assumed that spring hunting should not negatively influence reproduction if it is timed so that harvest of males occurs after the majority of mating activities have occurred (Isabelle et al. 2018). Vangilder and Kurzejeski (1995) estimated that no more than 30% of males could be harvested before there were negative effects on reproduction. However, recent research has begun to challenge these two assumptions. A recent study observed that wild turkeys gobble less on hunted areas than on nonhunted areas, and suggested hunting pressure may suppress gobbling as males are faced with a trade-off between maximizing reproductive success and minimizing their risk of predation or harvest (Wightman et al. 2019). Wild turkeys gobble to attract females (Healy 1992) but gobbling may also increase probability of detection by a predator (Zuk and Kolluru 1998). If wild turkeys choose to avoid predation by reducing gobbling activity, this could lead to lowered

reproductive success by attracting fewer females that are ready to mate (Wightman et al 2019). Although it is possible that hunting decreases gobbling activity because males change their behavior to avoid harvest, it is also possible that gobbling activity is decreased because gobbling males are more likely to be harvested and removed from the population. If the dominant males in a population are harvested before they have the chance to mate with females and subordinate males are unable to mate, this could lead to lower reproductive success and recruitment (Kurzejeski and Vangilder 1992, Norman et al. 2001). In addition, solitary male wild turkeys are known to have less mating success as females are less likely to mate with them than they are with males in sibling coalitions (Krakauer 2005). Thus, break-up of male sibling coalitions via harvest could result in reduced densities of dominant male wild turkeys that are able to mate with females or less attractive individual males with which females want to mate, leading to lowered population-level reproductive success (Krakauer 2005). This research demonstrates the importance of the roles of males in regard to reproductive success and the need to better understand the reproductive ecology of males from a management perspective.

Hunting pressure has been observed to affect a variety of behaviors across different taxa including decreased calling in several species of African monkeys (Croes et al. 2006), increased movement rates in elk (*Cervus elaphus*: Cleveland et al. 2012,), and altered space use based on perceived risks in black bears (*Ursus americanus*; Stillfried et al. 2015). In some cases, hunting pressure results in a direct negative impact on populations as behavioral changes can result in increased risk of harvest (Cleveland et al. 2012). Hunting pressure can also indirectly affect populations by causing changes in behavior that reduce the risk of survival or successful reproduction (Croes et al. 2006,

Cleveland et al. 2012, Stillfried et al. 2015). In addition to the differences in gobbling activity observed by Wightman et al. (2019) between hunted and non-hunted populations, recent research has shown that male wild turkeys may alter movements and resource selection as a result of hunting pressure (Wakefield et al. 2021). Male wild turkeys have been observed increasing daily movements as well as range size during the spring (Kelley et al. 1988, Hoffman 1991, Godwin 1994, Byrne et al. 2015, Collier et al. 2017, Chamberlain et al. 2018), and it has been widely assumed increased movements are a result of reproductive behaviors (Kelley et al. 1988). However, this result has not been universal across studies which may indicate that other factors are responsible for increased movements, including hunting pressure. These studies highlight the need for the collection of baseline data on turkey behavior in the absence of hunting pressure.

Given the number of studies that have recently reported changes in behavior of wild turkeys in the presence of hunting, research on male wild turkeys needs to focus on better understanding factors influencing reproductive season behaviors of male wild turkeys in the absence of hunting pressure. The effects of hunting pressure interfere with the ability to understand how other factors may be influencing wild turkey behavior. The opportunity to conduct research on nonhunted populations is rare as most populations of wild turkeys in North America are hunted. However, better understanding the mechanisms behind reproductive season movements and behaviors in the absence of hunting pressure is critical in order to provide baseline data on the reproductive ecology of male wild turkeys. My thesis will focus on assessing several factors influencing the space use of male wild turkeys during the mating season and summer non-mating season in a nonhunted population. My first chapter assesses seasonal differences in space use of

male wild turkeys while my second chapter works to determine if cooperative mating

strategies and kin selection are operating in a population of male wild turkeys living in a

heavily forested ecosystem.

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Chapter 2: Seasonal Variation in Male Wild Turkey Space Use Patterns

Introduction

Understanding the space use and ranging behavior of animals throughout all stages of their annual cycle is necessary for informing management and conservation strategies. Animal space use is the result of adaptations to dynamic environmental characteristics, biotic interactions, and intrinsic factors (Börger et al. 2008, Horne et al. 2008, Viana et al. 2018). Environmental factors include the distribution of forage (Bergerud 1974, Fridell and Litvaitis 1992, Schoepf et al. 2015), cover (Brahsares 2002 and Hayes 2006) and sites suitable for reproduction and nesting (Borger et al 2008). Biotic interactions include territoriality and competition with conspecifics, distribution and availability of receptive mates, and proximity to predators (Wauters et al. 2001, Dahle and Swenson 2003, Horne et al. 2008, Giuggioli and Kenkre 2014). Intrinsic factors can include sex, age, mental condition, and physical condition (Börger et al. 2008, Viana et al. 2018). Understanding causes of a specific animal's space use can be challenging because of the great variation in possible factors that can influence space use.

Space use by many animals varies seasonally and may be related to changes in habitat preferences, the availability, abundance, and distribution of resources (Van Beest et al. 2010), or reproductive activities (Dahle and Swenson 2003, Viana et al. 2018). Wild turkeys are a popular game species that use a polygynous-promiscuous mating system in which both sexes can potentially have multiple partners during a single mating season and no pair bonds are formed (Healy 1992). In order to maximize their reproductive success, the primary objective of males during the mating season should be maximizing encounters with females who are receptive to courtship and mating (Dahle and Swenson

2003). Because male wild turkeys do not participate in nest or offspring care and therefore are not spatially restricted to a nest site, a male's primary focus after breeding season should shift from locating and courting females to a maintenance state focused on foraging (Holdstock et al. 2006 and Byrne et al. 2015). This shift in resource priorities from mating to foraging should affect daily movement strategies of males, resulting in differences in how they use space within their home range between mating and non-mating seasons. Female wild turkeys are a widely dispersed and dynamic resource, thus during the mating season male wild turkeys will likely need to traverse larger portions of their annual range daily in order to maximize their opportunity of encountering receptive females (Erlinghe and Sandell 1986, Dahle and Swenson 2003). During summer non-mating periods, focal food resources in forested environments are likely more temporally and spatially predictable than females during the mating season, so male wild turkeys may not have to traverse as much of their annual range on a daily basis in order to meet their foraging needs as they do in order to meet their reproductive needs during the mating season (Roth and Vetter 2008).

Concomitant with these expectations, increased daily movements of male wild turkeys during the mating season relative to non-mating seasons have been widely reported (Kelley et al. 1988, Hoffman 1991, Godwin 1994, Collier et al. 2017), as has distance between consecutive nightly roost locations (Byrne et al. 2015). Greater movement during the mating season is often attributed to reproductive behaviors (Godwin 1994, Gross et al. 2015b), such as searching for females (Kelley et al. 1988) and the need to visit multiple display sites (Everett et al. 1985, Healy 1992, Badyaev et al. 1996). Additionally, use of widely dispersed roost locations may help maximize

opportunities of encountering receptive females (Byrne et al. 2015, Wakefield et al. 2020), as male wild turkeys frequently call from roosts, which provides an elevated location safe from predators that maximizes sound propagation and allows possible mates to better hear their calls (Mathevon et al. 2015, Boncoraglio and Saino 2007, Ey and Fischer 2009). However, it is important to acknowledge the possible confounding effects of hunting on the interpretation of these observations, as recent research has shown that hunting may affect the behavior of male wild turkeys (Wightman et al. 2019, Wakefield et al. 2020). For example, Wightman et al. (2019) noted decreased gobbling on hunted sites compared to non-hunted sites and Wakefield et al. (2020) found possible differences in roosting behavior as a result of hunting pressure. Thus, in order to better determine if reproductive behavior is a primary driver of male wild turkey movements during spring, it is critical to conduct research on space use on a nonhunted population to eliminate possible confounding effects of hunting pressure.

In studies comparing behavior between the reproductive and non-reproductive periods, it is important that observed behaviors be accurately delineated into mating and non-mating periods. Gobbling is a vocalization used by male wild turkeys to attract females for mating (Healy 1992), often elicited in response to female vocalizations (Scott and Boeker 1972), increased testosterone during the mating season (Lisano and Kennamer 1977), and female receptivity (Miller et al. 1997, Norman et al. 2001). Autonomous recording units (ARUs; Colbert et al. 2015) have been determined to be an effective way of remotely monitoring gobbling activity and have been used in recent studies that have worked to identify temporal variation in gobbling activity (Chamberlain et al. 2018, Wightman et al. 2019, Wakefield et al. 2020). Because increased gobbling

activity is associated with courtship behaviors, it serves as a good indicator of the mating season. Using gobbling data provides a means to objectively identify mating season timing specific to a study area.

I monitored male wild turkey space use via GPS telemetry during the spring mating and summer non-mating seasons in a pine-dominated landscape in the Southeastern United States to test hypotheses based on the idea that changes in resource needs and availability between mating and summer non-mating seasons leads to differences in the way male wild turkeys use space between seasons. In order to gather data on male wild turkey movements without the confounding effects of hunting pressure, I conducted research on a nonhunted population of wild turkeys. I used gobbling data collected via ARUs to accurately delineate peak mating and summer non-mating seasons in each year of the study. I hypothesized that median daily range size of male wild turkeys would be larger during the mating season than the summer non-mating season as searching for receptive females during the mating season will require males to traverse large portions of their annual range each day. Conversely, I hypothesized that median daily range size during the non-mating season would be smaller as male focus should shift from searching for females to foraging. Concomitantly, I hypothesized that male wild turkeys would use widely dispersed roost locations during the mating season, resulting in further distance between consecutive nightly roost locations used during the mating season than during the non-mating season (Byrne et al. 2015). A variety of dynamic factors such as female availability, male competition, and fluctuating hormone levels could influence daily behaviors during the mating season (Chamberlain et al. 2018). Thus, I hypothesized greater fluctuation in daily range size during the mating

season relative to the summer non-mating season, leading to more significant temporal autocorrelation in daily range sizes during the summer non-mating season compared to the mating season. Finally, I hypothesized that male wild turkeys would consistently use the same portion of their seasonal range on a daily basis during the mating season in order to maximize their chances of encountering receptive females. Conversely, during the summer non-mating season, I hypothesized that male wild turkeys would use smaller portions of their range for several

days in a row if they were exploiting a productive food patch before moving to a different portion of their range.

Methods

Study Site

All data was collected on the Savannah River Site (SRS), a 78,000 ha Department of Energy property located in the coastal plain of South Carolina (Figure 2.1). Approximately 94% of SRS is forested with loblolly pine (*Pinus taeda*, 35%) as the most abundant species, followed by longleaf (*Pinus palustris*, 23%) and bottomland hardwood forests (20%). Long-leaf scrub oak, mesic pine hardwood, upland hardwood, and cypress tupelo make up the remainder of the forest types. Twenty-five percent of the site is covered by wetlands (bottomland and swamp forest, creeks, streams, upland depressions, and Carolina Bays). Before 1951, SRS was dominated by agriculture, but since then, most management of SRS has been taken over by the USDA Forest Service and increased forest cultivation has resulted in increased wildlife populations. SRS now serves as important wildlife habitat for a variety of species including wild turkeys (White and Gaines 2000).

Sixty percent of the forested areas have been managed intensively for Red-cockaded Woodpeckers (*Leuconotopicus borealis*) resulting in long-rotation longleaf (120 years) and loblolly pine (80 years) stands while the remaining 40% of forested areas are managed on 50-year rotations. The recovery of Red-cockaded Woodpeckers has resulted in frequent prescribed fire (3-5 year burn rotation; White and Gaines 2000).

Since 1951, there has been limited hunting pressure on SRS. The only wild turkey hunting occurs during an annual 2-day event for 25 mobility-impaired hunters. This hunt began in 2002 and has happened every year except for 2020 and 2021. The hunt normally occurs during mid-April and only takes place on a small portion of the site. On average, 25-40 wild turkeys are harvested during the hunt. The low hunting pressure on SRS makes it an ideal location for collecting baseline data on wild turkey movements and behavior.

Tagging and Telemetry

During January-March 2020 and December-March 2021, before the breakup of winter flocks, I captured turkeys using rocket nets. I scouted potential trap sites and baited these sites with cracked corn. Potential trap sites were open areas where turkey sign or activity were observed. Most captures took place in forest openings, powerline right-of-ways, and food plots. Upon capture, I determined age of the birds based on the barring of the ninth and tenth primary feathers (Pelham and Dickson 1992) and banded all birds with a numbered aluminum leg band. I took a small blood sample (<0.1 mL) from the brachial vein or medial metatarsal vein of each bird using a needle and capillary tube (Owen 2011). I fitted adult males with a backpack style GPS transmitter (Guthrie et al. 2011; Lotek Wireless, Newmarket, ON, Canada). I programmed GPS transmitters to

record locations hourly from 0500 - 2000 as well as one roost location at 2359 until the transmitter battery died or the transmitter was recovered (Chamberlain et al. 2018). I monitored turkeys 2-3 times per week with a 3-element handheld antenna and receiver and remotely downloaded GPS locations approximately once per week from 1 March-1 August.

Mating Season Identification

In order to differentiate the mating season from the summer non-mating season, I collected and analyzed data on male turkey gobbling patterns. I collected gobbling data via ARUs (Wildlife Acoustics Song Meter SM3 and SM4) that were deployed from 1 March-30 June annually. I placed ARUs approximately 3 m off the ground on the trunks of pine trees to minimize potential human or animal interference. I attached a microphone to the ARU and placed it on the trunk of the tree at a height of 6-9 m to increase the sampling range of the ARUs (Colbert et al. 2015, Wightman et al. 2019). I deployed 30 ARUs on SRS at sites where turkey activity was previously observed. I placed autonomous recording units >600 m apart to prevent gobbles from being recorded on multiple units simultaneously (Colbert et al. 2015). I programmed units to record sound data from 0500-1000 in 2020 and 0500-1100 in 2021 (Wightman et al. 2019) as the majority of gobbling occurs within a few hours of sunrise (Colbert 2013). I changed SD cards and batteries in the ARUs approximately once per month (Wightman et al. 2019).

Recordings from the ARUs were analyzed using a convolutional neural network (CNN) to identify possible gobbling events. A CNN is a deep learning algorithm used for image classification and pattern recognition. They are composed of multiple layers and work by extracting features from an input image, assigning weights, and training a model

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to classify images through back propagation (LeCun and Bengio 1995, Albawi et al. 2017). The ARU recordings were run through a CNN that was pre-trained to identify soundwaves associated with turkey gobbles (Wightman et al. 2022). There are numerous human and animal sounds with similar frequencies that can be falsely identified as turkey gobbles. Events selected as possible gobbles by the CNN were auditorily evaluated to ensure that the event was a true gobble and not a false positive (Wightman et al. 2019).

I fit a generalized additive mixed effects model to each year's data to model gobbling activity over time in each year using package "mcgv" (Wood 2011) in R (R Core Team 2020). I included a fixed effect for date and a random effect for individual ARU to correct for systematic variation between units resulting from uneven distribution of gobbling male turkeys across the landscape. Because the response variable, number of gobbles per ARU, was count data, I used Poisson regression. I used package ggplot2 (Wickham 2016) in R (R Core Team 2020) to visually examine model predictions to determine times of increased and decreased gobbling activity. Season boundaries were then set based on observed peaks in gobbling activity and mating season boundaries were set to encompass time periods with the greatest gobbling activity. For the purpose of these analyses, I attempted to set season boundaries in each year that resulted in mating and non-mating seasons of similar lengths. Season lengths were 7 weeks for the mating season and 7.5 weeks for the non-mating season in 2020 and 7.9 weeks for the mating season and 8.6 weeks for the non-mating season in 2021. Following peak mating season, mating activity does not abruptly stop. Instead, mating activities slowly taper off and end at different times for different individual males (Scott and Boeker 1972, Healy 1992, Chamberlain 2018). This results in continued gobbling activity after peak mating season,

making exact delineation of the mating and non-mating seasons based on gobbling activity difficult. To account for this, we included a transition period between the peak mating and summer non-mating seasons in each year. This transition period was excluded from analysis to ensure that data was representative of behaviors associated with peak mating and non-mating summer seasons, respectively.

Daily and Seasonal Range Estimation

Previous studies on turkey movements have quantified daily space use using the total daily distance moved, calculated by summing total step lengths (distance between consecutive GPS points) traveled in a day (Gross et al. 2015b, Collier et al. 2017, Chamberlain et al. 2018). However, theoretically, two birds could travel in different patterns during a given day (i.e., a straight line or a circular pattern) yet provide the same measure of total daily distance moved, despite using space in drastically different ways. Quantifying daily range size, defined as the total area traversed in a day, instead of total daily distance moved may provide more meaningful insight into how wild turkeys use space within their ranges.

I used Dynamic Brownian Bridge Movement Models (dBBMM; Kranstauber et al. 2012) to estimate the daily and seasonal utilization distributions (UDs) of males. A UD is a spatial probability distribution providing the relative probability of an animal being located at a given location, which can be used to estimate range (Worton 1989, Kranstauber 2012). Dynamic Brownian Bridge Movement Models are beneficial because they can account for behavioral changes along an animal's movement path as well as account for temporal autocorrelation in large datasets by conditioning UD estimation on an animal's movement path (Kranstauber et al. 2012). The dBBMM accounts for changes

in an animal's movement path by allowing the Brownian motion variance, a measure of irregularity, to vary along observed movement paths (Horne et al. 2012 and Kranstauber et al. 2012).

Following Byrne et al. (2019), I estimated daily space use for each turkey by first fitting a (dBBMM) to the full movement path of each turkey using a location error of 20 m, and constant window and margin sizes equal to 7 and 3 (Cohen et al. 2018). I estimated daily UDs on a 5 m^2 spatial grid based on movements between sunrise and sunset. I quantified daily ranges as the area within the 99% contour which provides a measure of the total area traversed in a day (Byrne et al. 2019). I implemented the same parameters for estimating seasonal range but quantified the area within the 95% contour to provide a measure of the total area traversed in a season. Days with less than 5 GPS fixes were excluded from analysis (Cohen et al. 2018).

Seasonal Differences in Daily Ranges

To test the prediction that daily ranges of male wild turkeys are larger during the mating season than the summer non-mating season, I used a generalized linear mixed effects model with a gamma link with a fixed effect for season and random effects for individual turkey and year. I chose to use a gamma distribution for this model because the roost distance data is continuous, non-negative, and right skewed. The model took the form:

Equation 1

$$Y = \beta_0 + \beta_1(Season) + Z_1(Individual\ Turkey) + Z_2(Year)$$

where Y is the daily range size, β_0 and β_1 are regression coefficients, Z_1 is a random effect for individual turkey, and Z_2 is a random effect for year.

To test the prediction that there would be greater temporal autocorrelation in the size of daily summer non-mating ranges compared to daily mating season ranges, I calculated autocorrelation functions (ACF) of daily range sizes for each male seasonally to determine the number of days that showed significant autocorrelation. Autocorrelation functions measure the relationship between an observation at time t and the observations at previous times (Boyce et al. 2010). ACF values close to one indicate a positive correlation while ACF values close to negative one indicate a negative correlation. ACF values close to 0 indicate no correlation.

Seasonal Differences in Roosting Behavior

To test the prediction that the distance between consecutive nightly roost locations would be larger during the mating season than during the summer non-mating season, I used the "XY to Line" tool in ArcGIS 10.7.1 (ESRI 2019) to measure linear distance between consecutive nightly roost locations (Gross et al. 2015b). I used a generalized linear mixed effects model with a gamma link to determine seasonal differences in distances between consecutive roost locations with a fixed effect for season and a random effect for individual turkey. I chose to use a gamma distribution for this model because the roost distance data is continuous, non-negative, and right skewed. The model took the form:

Equation 2

$$Y = \beta_0 + \beta_1(Season) + Z_1(Individual\ Turkey)$$

where Y is the distance between consecutive roost sites, β_0 and β_1 are regression coefficients, and Z_1 is a random effect for individual turkey.

Distribution of Space Use within Seasonal Ranges

To test the prediction that male wild turkeys use space within their seasonal ranges differently between the mating and summer non-mating seasons, I examined the daily dispersion of GPS locations. I assessed for each turkey and season, the dispersion of daily locations within seasonal ranges by treating each day's locations and all the other locations within a season as two parts of a multivariate point pattern. I calculated the difference in intensity of aggregation between the two parts of the point pattern as the differences in the univariate K-functions (Dixon 2001) between the parts for a range of distances using package "ecespa" (Rot et al. 2010) in R (R Core Team 2020). The univariate K -function estimates the expected density of locations withing a distance, r, around any randomly chosen location (Dixon 2001). The equation took the form:

Equation 3

$$D(r) = K_1(r) - K_2(r)$$

where $K_1(r)$ is the univariate K-function of the seasonal point pattern and $K_2(r)$ is the univariate K- function for the daily point pattern. Values near 0 indicate minimal difference in aggregation between daily locations and all other locations within a season and more negative values indicate a larger difference in aggregation between daily locations and all other location within a season. The range of distances for each turkey and each season were determined based on the median difference between either the x or y dimensions for each day (Lenz et al. 2015). I calculated the mean and range of daily aggregation values for each turkey and season and plotted them using package "ggplot2" (Wickham 2016) in R (R Core Team 2020). These plots allowed me to determine if daily aggregation values differed between the mating and non-mating season. I expected the

aggregation values to be closer to 0 for the mating season and more negative for the non-mating season.

Results

I trapped 10 adult male turkeys in 2020, one of which died after the mating season and thus did not provide summer data, and one of which died soon after trapping and did not provide any data. During 2021, I captured 25 adult males, of which 15 died or had transmitter malfunctions soon after trapping, resulting in their exclusion from all analyses. An additional male died after the mating season and thus did not provide summer data. I was able to gather data for both seasons for 17 males, and mating-season only data for 2 males. I gathered 3,494 total days of data, and after exclusion of days with <5 GPS fixes, this resulted in 450 days of mating season data in 2020, 660 days of mating season data in 2021, 464 days of summer non-mating season data for 2020, 605 days of summer non-mating season data for 2021, and 1,315 days of data from pre-breeding and transition periods in 2020 and 2021. During 2020 there were 21 total days or data that were excluded: 9 from the mating season, 4 from the summer non-mating season, and 8 from pre-breeding and transition periods. During 2021, no days had less than 5 GPS fixes, so all days were included in analysis.

Gobbling Data

I confirmed 42,733 gobbling events during 2020 and 19,590 gobbling events in 2021. For 2020, the spring mating season was set as 24 March – 13 May and the summer non-mating season was set as 10 June-31 July. For 2021, the spring mating season was set as 22 March -20 May and the summer non-mating season was set as 7 June-31 July (Figure 2.2).

Seasonal Differences in Daily Ranges

The median daily range size was 155.3 ha (range: 2.7 - 2632.9 ha) during the mating season and 70.7 ha (range 4.3 - 680.5 ha) during the non-mating season (Figure 2.3). The linear mixed model with a log transformation of daily range size showed season to be an important predictor of daily range size (β = -0.30, 95% CI: -0.33 - -0.27), with mating season daily range sizes larger than the summer non-mating season daily range sizes (Figure 2.4). On average, male wild turkeys decreased their median daily range size by 50.62% (range: 2.38 – 76.02%) from the mating to the non-mating season. There was a trend towards larger average daily mating season range sizes in 2020 (Figure 2.3), however, much of the difference in range sizes between years can be attributed to the movements of two males whose median daily range sizes during the mating season were 320.7 and 333.9 ha, respectively, which were higher than the average of the median daily range sizes of all other males during 2020 (average: 162.1 range: 113.2 - 301.1 ha). Two males accounted for 13 of 16 (81.3%) observations of daily range sizes > 1000 ha. The median seasonal range size was 627.5 (range: 354.0 – 3250.3) for the mating season and 453.1 (range: 147.0 – 747.4) for the non-mating season.

Only one individual exhibited autocorrelation in daily range size during the mating season, with a significant temporal lag of 2 days (Table 1), indicating that there is a large amount of variation in the size of daily ranges during the mating season which supports my original prediction. During summer, six individuals (33%) exhibited autocorrelation in daily range size, although, with the exception of one individual the significant temporal lag was $\leq$ 2 days (Table 1), indicating that there is also a large amount of variation in the size of daily ranges during the non-mating season,

contradicting my original prediction that there would significantly more autocorrelation in the size of daily summer ranges.

Seasonal Differences in Roosting Behavior

The median distance between consecutive nightly roost locations was 1.20 km (range: 0.002 - 6.17 km) during the mating season and 0.77 km (range:0.002 - 4.76 km) during the summer non-mating season (Figure 2.3). The generalized linear mixed effects model showed season to be an important predictor of the distance between consecutive nightly roost locations with a greater distance between consecutive nightly roosts in the mating season than the non-mating season (β = -0.40, 95% CI: -0.50 - -0.29).

Distribution of Space Use within Seasonal Ranges

There were no observable patterns when I plotted the average differences in aggregation intensity for each turkey and season which contradicts my original prediction that male wild turkeys would use space within their seasonal ranges differently between the mating and summer non-mating seasons (Figure 2.5). There is no evidence that indicates that male wild turkeys were consistently revisiting the same portions of their seasonal range on a daily basis during the mating season as this would have resulted in daily locations that were more dispersed throughout the seasonal range (Aggregation value close to 0). There was also no evidence suggesting male wild turkeys were consistently using smaller portions of their seasonal range for multiple days as this would have resulted in greater aggregation of daily locations compared to all other seasonal locations (Increasingly negative aggregation value). There was a lot of overlap between seasons in the maximum and minimum values at each distance for most of the males,

indicating that there was considerable daily variation in how males used space within their ranges in both seasons (Figure 2.5).

Discussion

Hunting has been shown to affect male wild turkey behavior during the spring (Wakefield et al. 2019, Wightman et al. 2019). The absence of hunting on SRS allowed me to draw inferences on seasonal variation in male wild turkey movements and space use without the confounding effects of hunting. Despite the lack of hunting on SRS, the majority of male turkeys still traversed more area during the spring mating season than during the summer non-mating season, suggesting that reproductive behaviors are likely one of the main drivers of male wild turkey space use during the mating season. My prediction that daily range size would be larger during the mating season as compared to the non-mating season was supported. Male wild turkeys decreased median daily range size between the mating and non-mating season by an average of 50.62%, and 83% decreased their seasonal range size from the mating season to the non-mating season. Similarly, my prediction that there would be greater distances between consecutive nightly roost locations in the mating season compared to the non-mating season was supported, and similar to Wakefield et al. (2019), I observed male eastern wild turkeys moving long distances (>4km) during the mating season.

Animals form home ranges because site familiarity increases fitness (Spencer 2012). Fitness benefits include increased survival due to decreased predation, success in dominance interactions, and improved knowledge of foraging locations (Piper 2011, Forrester et al. 2015). Expanding a home range is typically considered disadvantageous unless it no longer meets an individual's needs. Wild turkeys may need to expand their

daily ranges as they traverse more area during the mating season in search of receptive

females, and then decrease this area after the mating season as they no longer require the

same amount of area to meet their non-mating season needs. (Kelley et al. 1988, Godwin

et al. 1994). The increase in range size of the majority of the birds during the mating

season is consistent with several previous studies on wild turkeys and indicates that male

wild turkeys may expand their daily ranges during the spring as a result of reproductive

activities. Increased distance between consecutive nightly roosts has been correlated to

increased range size (Gross et al. 2015b). As males move around their range searching for

females, they are more likely to use consecutive nightly roost sites that are far apart

Wakefield et al. (2019) proposed that calling from one roost and then moving a great

distance to another roost to call may be a reproductive strategy used by eastern wild

turkeys to increase the number of receptive females that hear the calling, and can also

likely be explained by the availability and distribution of necessary mating resources such

as receptive females (Byrne et al. 2015, Gross et al. 2015b, Wakefield et al. 2019).

Despite variation in the amount of space male wild turkeys use during the mating

and the non-mating season, my results do not indicate that patterns of space use within

seasonal home ranges varies between the mating and the non-mating season. My

prediction that there would be greater temporal autocorrelation in the size of daily ranges

during the non-mating season was not supported. There was also no observable pattern in

the average aggregation intensity of daily locations between the mating and non-mating

season. Other species, such as Trumpeter hornbills (*Bycanistes buccinator*; Lenz et al.

2015), have shown clear differences in their space use within seasonal home-ranges.

During the mating season, trumpeter hornbills exhibit a stationary home range pattern in

which their daily locations are relatively well dispersed throughout their mating season range, but during the winter, they shift the locations of their daily ranges to a different area every few days. I expected to see a similar behavior in male wild turkeys, however there was no clear difference in average aggregation intensity between seasons and there was a significant amount of day-to-day variation in intensity of daily aggregation of locations within both the mating and non-mating season. The testosterone levels of male turkeys vary greatly from day to day during the mating season possibly resulting in increased mating activities on days when testosterone levels are higher (Chamberlain et al. 2018). Chamberlain et al. (2018) proposed that the pulsatile testosterone levels of male turkeys during the mating season likely explained variation in daily gobbling activity of male turkeys during the mating season. I believe that the daily fluctuation in testosterone levels could also explain the high variation in intensity of aggregation of daily locations of male wild turkeys during the mating season. The low temporal autocorrelation in the size of daily mating season ranges was consistent with my prediction and is likely also related to the pulsatile testosterone levels of male wild turkeys (Chamberlain et al. 2018).

During the summer, I predicted that a shift in resource priorities from mating to foraging would result in differences in space use of male wild turkeys compared to the mating season. Because males would no longer be searching for females with which to mate, I predicted that this would translate to smaller daily ranges sizes and smaller distances between consecutive nightly roost locations during the summer non-breeding season. While I did find these predictions to be true, I also predicted that if males were exploiting a productive food patch for several days at a time before moving to a different portion of their range, it would result is greater temporal autocorrelation between the size

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of daily non-mating season ranges than the size of daily mating season ranges as well as greater intensity of aggregation of daily locations during the summer non-mating season. These predictions were not supported, possibly indicating that foraging resources were relatively evenly distributed or that foraging areas were not the only important factor determining space use of male wild turkeys during the summer non-mating season. From my results, it appears that male wild turkeys may distribute their time more evenly across their summer range then I predicted. There are a number of factors that could affect space use of male wild turkeys including physiological factors (Badyaev et al 1996), social status (Badyaev et al. 1996, Rolando 2002), environmental conditions (Rolando 2000, Collier et al. 2017), habitat structure (Rolando 2002), and predator-prey interactions (Rolando 2002). Even though food availability has been shown to be one of the primary determinates of space use in birds (Rolando 2002), any combination of these dynamic factors may determine what is considered a favorable range on any given day and may explain the larger amount of variation that I observed in intensity of aggregation of daily locations and lack of temporal autocorrelation during the non-mating season. (Rolando 2002, Collier et al 2017).

While studies have widely reported increased movements of males during the spring (Hoffman 1991, Godwin 1994, Gross et al. 2015a, Gross et al. 2015b, Collier et al. 2017, Chamberlain et al. 2018), results show that summer home range size may be the same or larger than mating season ranges (Porter 1977, Everett et al. 1979, Miller et al. 1997, Grisham et al. 2008). Unique from these studies, I differentiated mating from non-mating seasons based on the timing of gobbling that occurred on my study site rather than assuming dates for mating and non-mating seasons based on approximate timing of

possible reproductive activities. I set the mating season dates to only encompass weeks where gobbling activity peaked and set the non-mating season to start after a transition period that ensured all mating activities were complete. Because previous studies did not base season boundaries on site specific reproductive behaviors, their results likely included data from pre-mating or post-mating periods. Additionally, without including a transition period between the mating and non-mating period, it is possible that the summer period included days where mating activity was still occurring, possibly leading to inflated summer home range sizes. Studies looking at seasonal movements of male wild turkeys have often set mating season and non-mating season boundaries that are different lengths (Everett, et al. 1985, Miller et al. 1997, Grisham et al. 2008). I used gobbling data specific to my study site and standardized the length of the mating and non-mating seasons, which provides evidence that daily range expansion actually occurred during the mating season.

My study provided evidence that male wild turkeys expand their daily and seasonal ranges during the mating season, even in the absence of hunting pressure. This indicates that reproductive behaviors are likely a main driver of increased movements and space use during the spring. My results were consistent with other studies that have reported significant variation in the daily movements and space use of wild turkeys during the spring (Collier et al. 2017). Additionally, my results also showed that there is significant variation in daily space use in the non-mating season as well. Factors affecting the movements and space use of male wild turkeys during the summer have received comparatively less attention than factors affecting spring movements. The factors determining space use are likely specific to site and individual and may vary greatly from

day to day. Given this site and individual variation in factors affecting space use, managers should focus on better understanding factors determining space use in their specific population of wild turkeys and create site-specific management strategies based on these factors. If possible, it would likely be beneficial for future studies to delineate study seasons based on site-specific reproductive behaviors such as gobbling chronology. Future research should continue gathering data on male wild turkeys in nonhunted populations in order to gain a better understanding of factors affecting wild turkey behaviors without the confounding effects of hunting.

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Tables and Figures

Table 2.1. Temporal autocorrelation (days) of daily range sizes during the mating season and the summer non-mating season by male wild turkeys tracked with GPS telemetry on the Savannah River Site, South Carolina, 2020-2021.

Turkey ID	Year	Significantly Autocorrelated Days	
		Mating	Summer
61241	2020	0	0
61242	2020	2	2
61243	2020	0	1
61289	2020	0	0
61297	2020	0	0
61303	2020	0	0
61308	2020	0	NA
61307	2020	0	0
61311	2020	0	0
47401	2021	0	0
47402	2021	0	1
47403	2021	0	0
47409	2021	0	1
47417	2021	0	0
47418	2021	0	0
47427	2021	0	0
47428	2021	0	0
47441	2021	0	1
47463	2021	0	6
47472	2021	0	NA
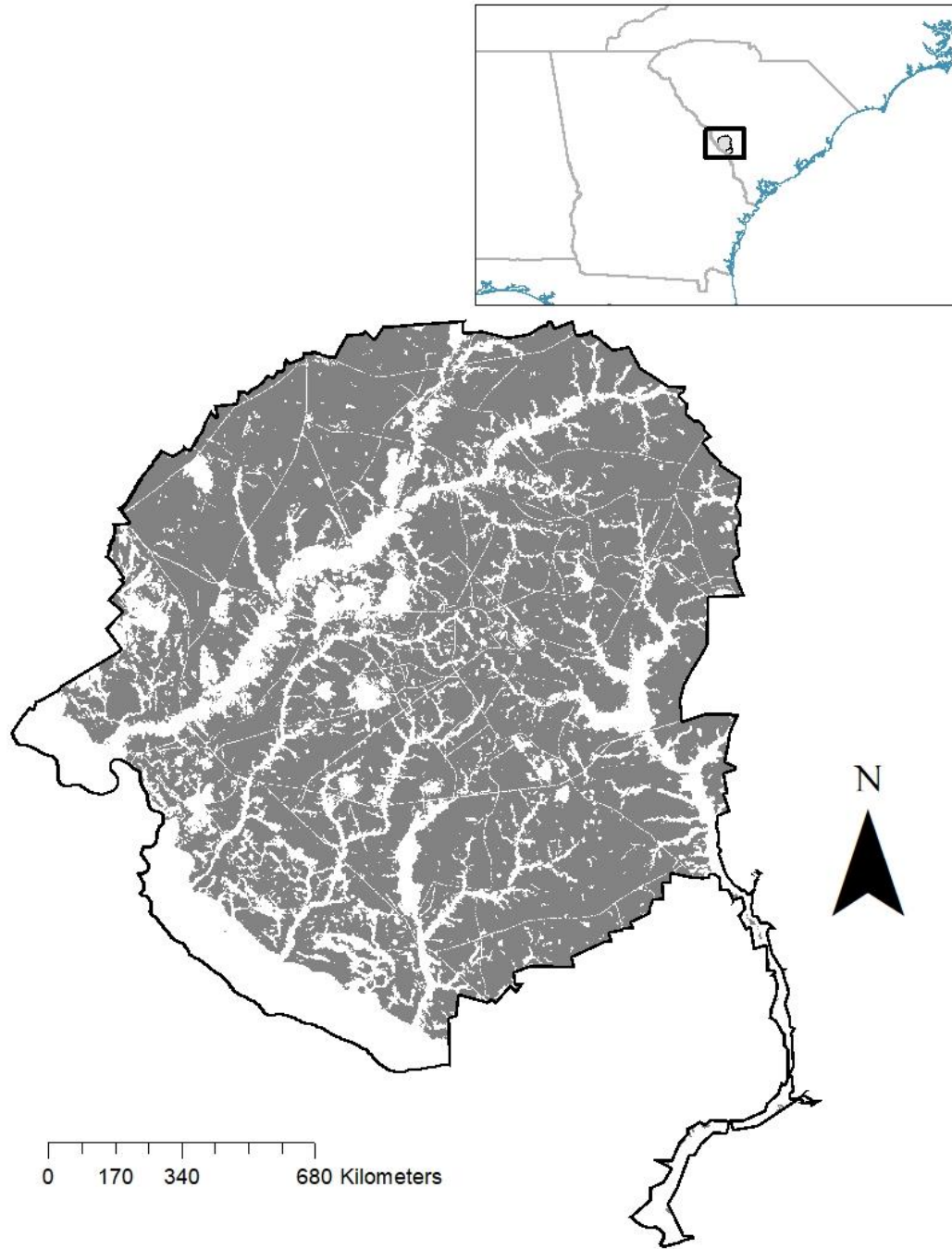
Figure 2.1. Map of the Savannah River Site located on the Georgia-South Carolina border and encompassing parts of Aiken, Allendale, and Barnwell Counties in South Carolina where all research took place. Gray areas indicate all forest types and white areas indicate all other cover types.
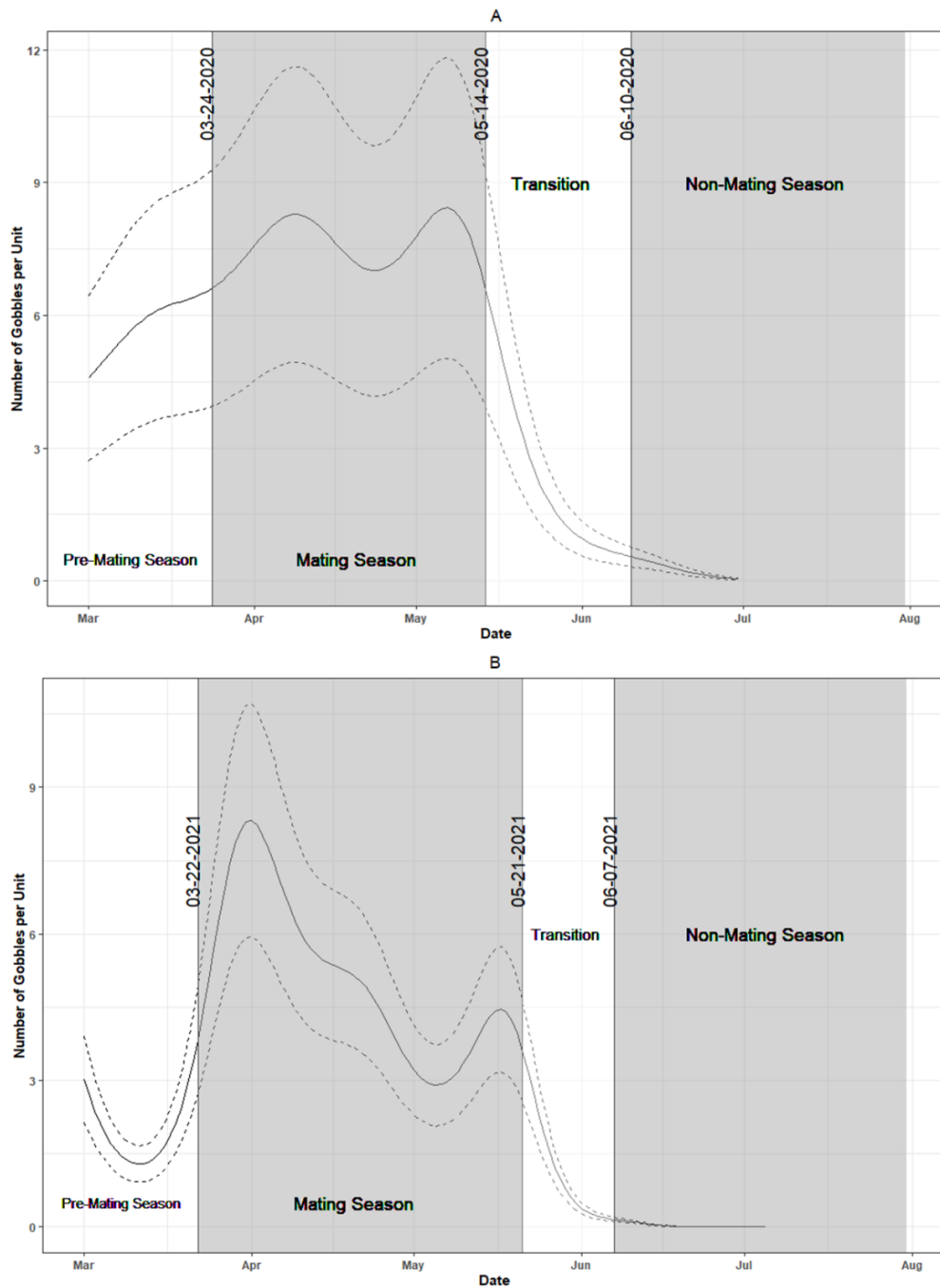
Figure 2.2. Delineation of (A) 2020 and (B) 2021 mating and non-mating season on the Savannah River Site, South Carolina and gobbling activity from autonomous recording units. based on peaks in gobbling activity. In 2020, the mating season encompassed times when estimates gobbles per unit ≥ 7, and in 2021 encompassed times when the estimated number of gobbles per unit was ≥ 4.
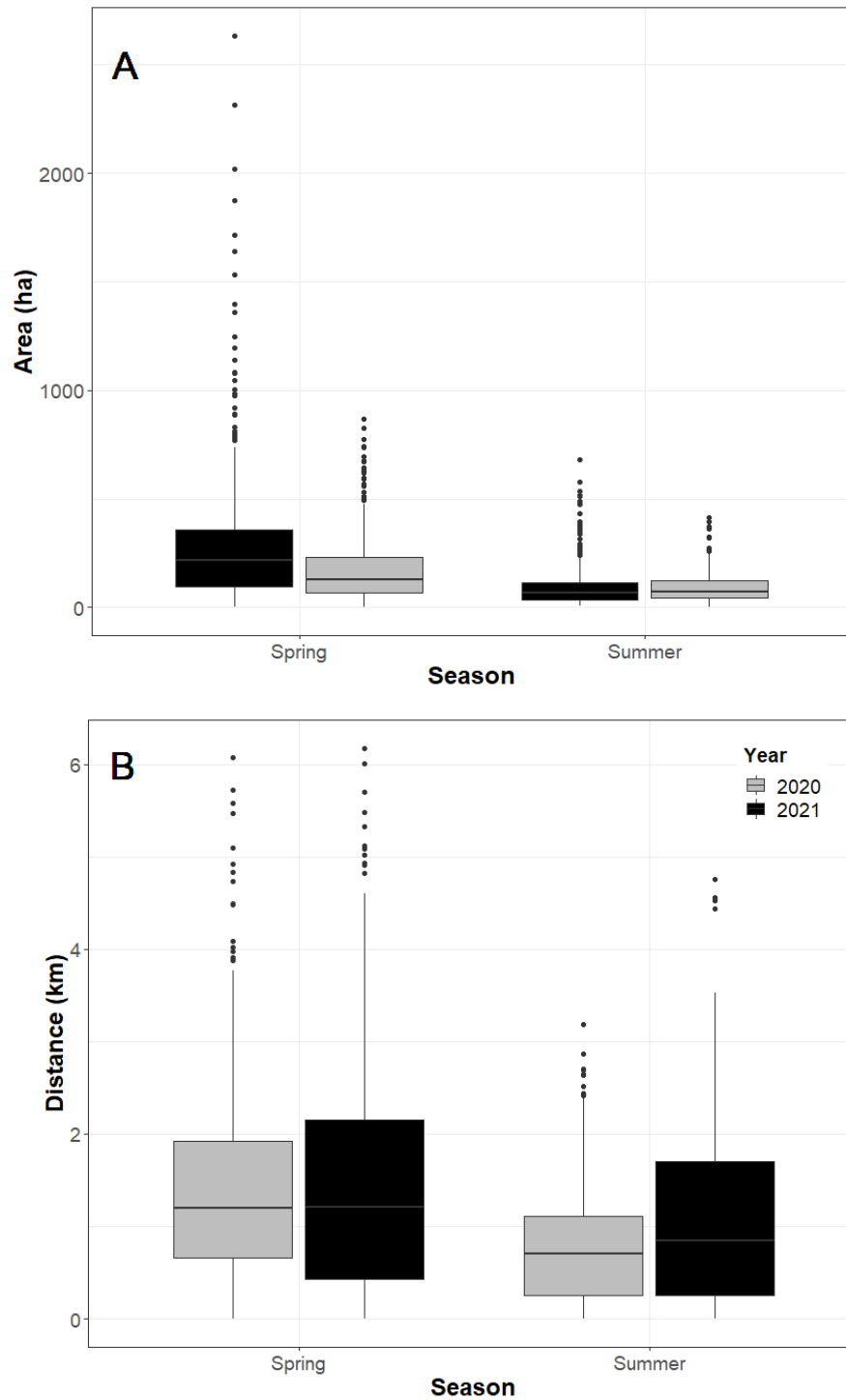
Figure 2.3. Boxplots of daily range size (A) and distances between consecutive nightly roost locations (B) for male wild turkeys tracked with GPS telemetry during the spring mating season and summer non-mating seasons on the Savannah River Site, South Carolina, during 2020 and 2021.
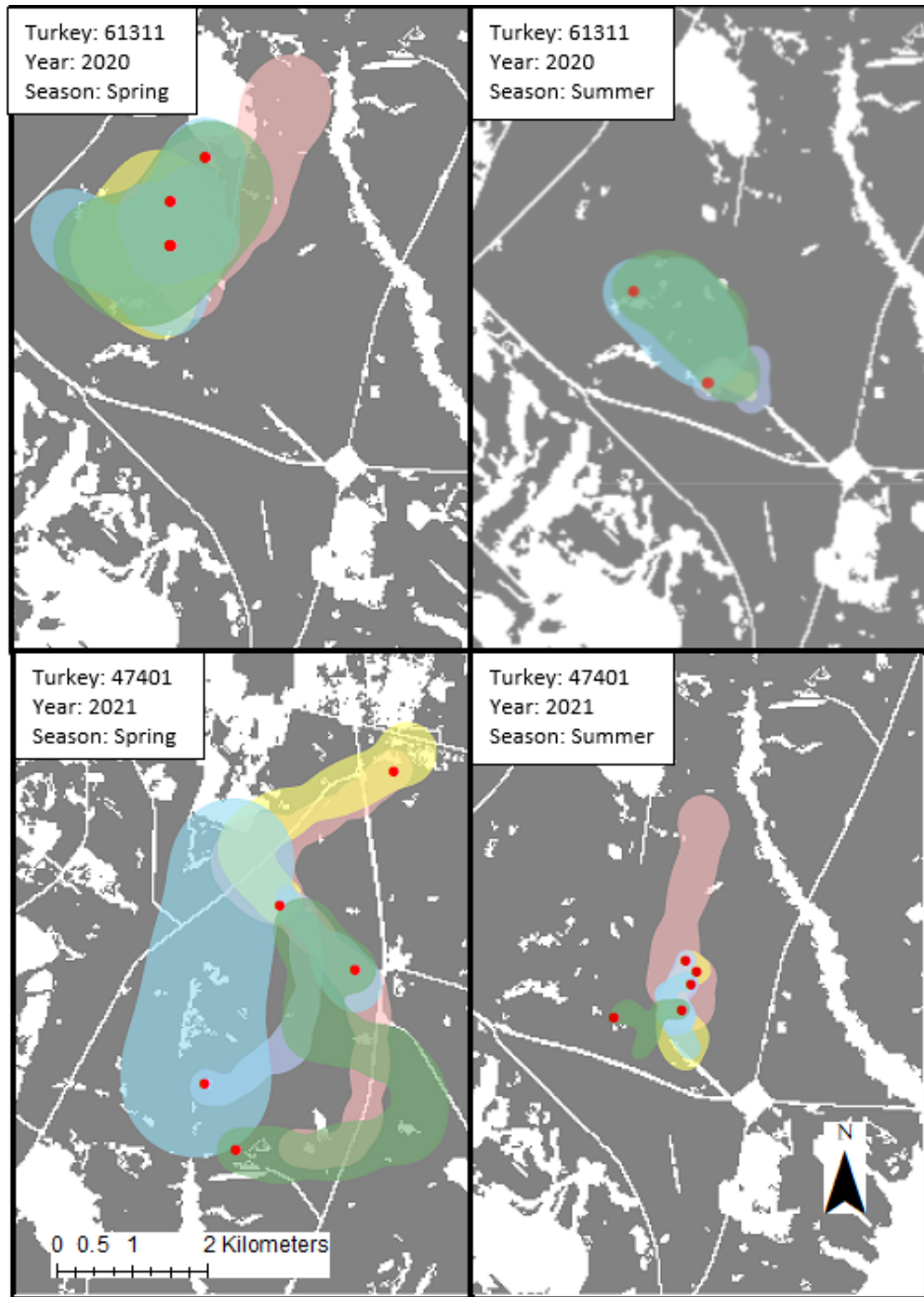
Figure 2.4. The top two panels show five consecutive daily ranges and roost locations of turkey 61311 during the spring mating and summer non-mating seasons of 2020 on the Savannah River Site. The bottom two panels show five consecutive daily ranges and roost locations of turkey 47401 during the spring mating and summer non-mating seasons of 2021 on the Savannah River Site. Each different color polygon represents a different daily range. Red points represent consecutive nightly roost locations.
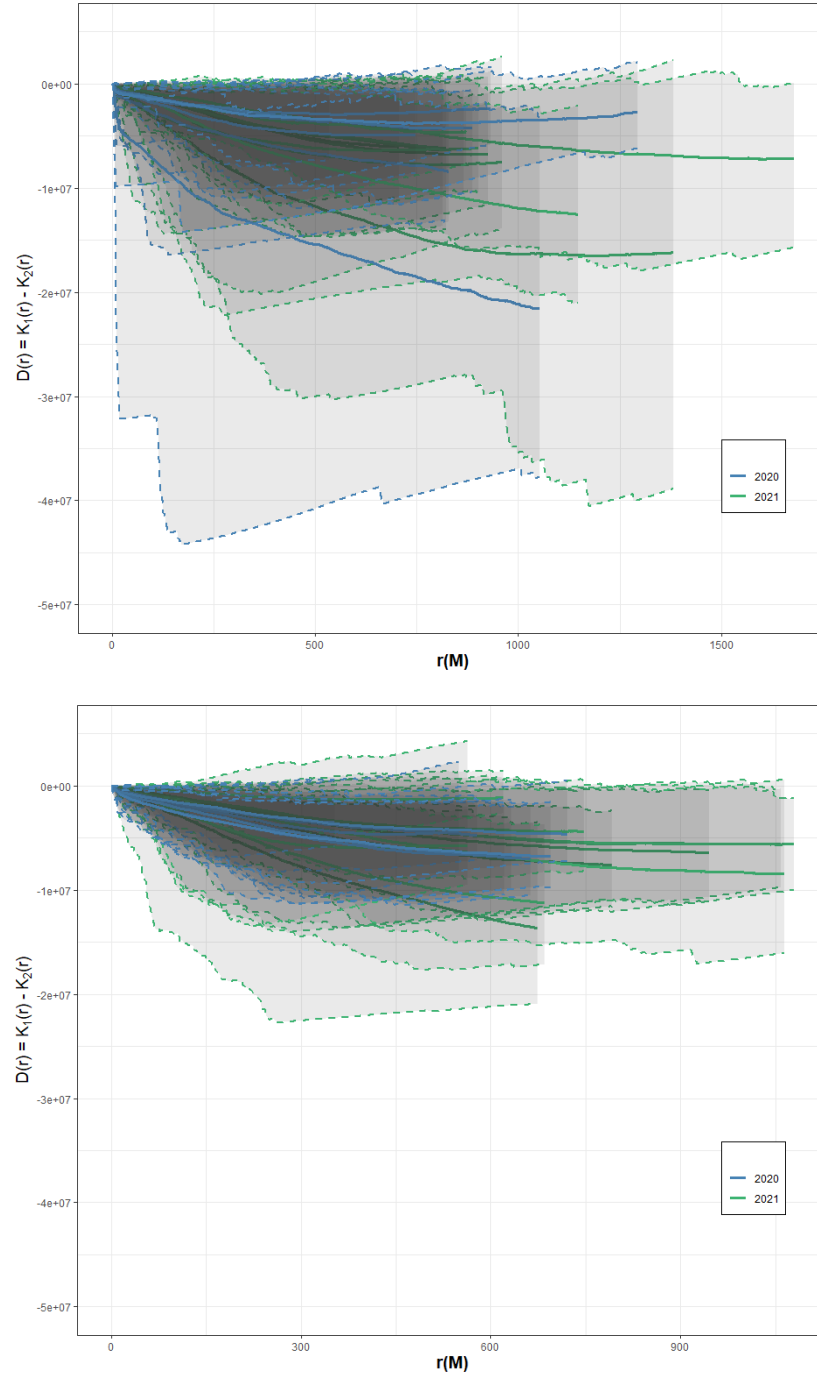
Figure 2.5. The panel on the top shows the average difference between K- functions for daily locations and all other mating season locations for male wild turkeys on the Savannah River Site in 2020 and 2021. The dotted lines indicate the maximum and minimum value calculated at each distance for each turkey. The gray shaded area represents the range of values for each male. The panel on the bottom shows average difference between K- functions for daily locations and all other non-mating season locations.

Chapter 3: Do Eastern Wild Turkeys Show Evidence of Kin Selection and Cooperative Courtship?

Introduction

A variety of environmental factors have been found to shape the evolution of avian mating systems. (Verner and Willson 1966, Emlen and Oring 1977, Wittenberger 1978). Resource availability, density, and dispersion are considered key to the development of mating systems as they control the degree to which an individual can control and possibly monopolize mates or resources necessary for successful reproduction. This ability to monopolize a resource is one of the most important factors in the evolution of polygynous mating systems in which males' mate with multiple females (Emlen and Oring 1977). Polygyny is likely to evolve when necessary resources like food and mates are spatially aggregated because it allows for better control of resources by males (Verner and Willson 1966, Emlen and Oring 1977). There are several different variations of polygynous mating systems that are differentiated by the method in which males control females (Emlen and Oring 1977). Many polygynous species also exhibit promiscuity, which is characterized by the lack of a long-term bond between males and females (Wittenberger 1978).

Wild turkeys inhabit a wide variety of habitat types in North America, and aspects of their social structure and mating systems may vary across habitat types (Watts and Stokes 1971, Healy 1992, Krakaeur 2008). While all wild turkeys use a polygynous-promiscuous mating system, variations in courtship behavior have been observed between subspecies living in different habitat types (Healy 1992). For example, male Rio Grande turkeys (*Meleagris gallopavo intermedia*) inhabiting open grassland habitats form leks (Watts and Stokes 1971, Healy 1992). A lek is a communal display ground in

which males display in groups and females visit the display grounds only to select a mate. A lek mating system is also characterized by unequal mating success among the males at the lek (Wiley 1978). A traditional lek-based mating system is advantageous for breeding in open, dry habitats where necessary resources are only available for a short time as leks allow females to be ready for breeding very quickly since all mating is done in a common area. Leks also allow for predator detection at greater distances in open habitats (Watts and Stokes 1971, Wiley 1978). In contrast, male eastern wild turkeys in forested ecosystems do not use communal display sites and are thought to use either an exploded lek mating system, or engage in a form or resource-defense polygyny (Healy 1992). In exploded leks, males display individually or in small groups at widely dispersed locations, and female mate choice is only based on male characteristics. In resource defense polygyny, males defend necessary resources or mates from other males and females select a mate based on the resources the male controls rather than the characteristics of the male (Alonso et al. 2012). Because male wild turkeys do not engage in prenatal care and have no connection to the female after mating (Healy 1992), wild turkeys are more likely to use an exploded lek system as opposed to resource-defense polygyny.

Despite variation in mating systems, the formation of sibling coalitions has been considered ubiquitous across ecosystems and subspecies (Healy 1992). However, Rio Grande wild turkeys are the only subspecies of turkeys in which apparent sibling coalitions have been observed participating in cooperative courtship, wherein, only the dominant sibling mates. While subordinate siblings assist in attracting and defending females from other males, they do not actually get the opportunity to mate themselves

(Watts and Stokes 1971, Krakauer 2005). Watts and Stokes (1971) observed this behavior in a population of Rio Grande turkeys in Texas on the Welder Wildlife Refuge. The relatedness of male coalitions has not been directly investigated in any subspecies other than Rio Grande turkeys. Krakauer (2005) conducted research on an introduced population of Rio Grande turkeys in California and provided evidence to support the hypothesis that kin selection (Hamilton 1964) may account for this strategy in wild turkeys. Kin selection is a concept that favors genetic success over reproductive success. The concept of kin selection states that individuals can pass on their genes indirectly by helping a close relative reproduce through altruistic behavior (Hamilton 1964). Since the goal of reproduction is to pass on genes, siblings are still succeeding in this goal if they are helping another sibling reproduce since all the siblings share some of the same genes that are being passed on by the reproducing sibling. Both Watts and Stokes (1971) and Krakauer (2005) studied Rio Grande turkeys in similar open habitat types. Both the Welder Refuge in Texas (Watts and Stokes 1971) and the Hastings Natural History Reserve in California (Krakauer 2005) are open grassland habitats with woody vegetation consisting mainly of small shrubs. Kin selection has been observed in several species of birds, including other Galliformes such as the black grouse (*Lyrurus tetrix*; Hoglund et al. 1999). However, like the Rio Grande turkeys observed by Krakauer (2005) and Watts and Stokes (1971), black grouse exhibits traditional lekking behavior and are observed in relatively open habitats (Hoglund et al. 1999). Given the variation in mating systems across subspecies of wild turkeys living in different habitats, it is possible that courtship behaviors could vary across subspecies and habitats as well. However, if kin selection is a

universally adaptive strategy for wild turkeys, the formation of coalitions of sibling males should be a trait that is observable across all habitats and subspecies.

While direct evidence of kin selection operating within a population is difficult to obtain because it requires a direct measure of reproductive success (Hamilton 1964, Krakauer 2005), I can test hypotheses regarding relatedness and social behavior of male wild turkeys during the mating season that could provide indirect evidence about the prevalence of cooperative courtship and kin selection in other populations. I used a combination of genetics and GPS tracking data to look for evidence of cooperative courtship and kin selection operating in a population of wild turkeys within a heavily forested ecosystem in South Carolina. I hypothesized that if cooperative courtship and kin selection operated in the population, sibling males would travel together as a coalition during all seasons as described in Rio Grande turkeys (Watts and Stokes 1971, Krakauer 2005). Additionally, I hypothesized that unrelated males captured together as part of winter flocks would disperse from each other prior to the mating season (Logan 1973).

Methods

Trapping, Blood Collection, and Telemetry

During January-March 2020 and December-March 2021, before the breakup of winter flocks, I captured turkeys using rocket nets at the Savannah River in South Carolina. Study area and capture details can be found in Chapter 2. I collected a blood sample from each turkey for use in genetics analysis. I restrained the turkeys by firmly grasping both legs and placing a black sleeve over the eyes. I laid them on their side and blood samples were taken either from the brachial vein on the ventral side of the wing, or from the medial metatarsal vein. I used an alcohol swab to prepare the site from which

blood was drawn and a 26-gauge needle was used to prick the vein. I collected blood in

capillary tubes, and following collection, applied pressure to the puncture site with an

alcohol swab to stop excess bleeding. I transferred blood in the capillary tube to an

Eppendorf tube with a Tris-EDTA lysis buffer solution (100mM Tris, 100 mM EDTA, 10

mM NaCl, 2% SDS), and shook and inverted to tube to ensure mixture of the blood and

lysis buffer. For genetics studies, Tris-EDTA lysis buffers are used to maintain the PH of

the solution as well as deactivate enzymes that cause degradation of DNA and RNA

(Lahiri and Schnabel 1993). I labeled blood samples with the GPS transmitter

identification number and stored them at room temperature (Owen 2011).

Genetics Analysis

Extraction of DNA from blood samples was conducted at Princeton University in

the lab of Dr. Bridgett vonHoldt. DNA was extracted from the blood using the Qiagen

DNeasy blood and tissue kit (Quiagen, Maryland, USA). The data was sequenced using

the bestRADseq method (Ali et al. 2015) and cleaned and processed using STACKS v2

(Catchen et al. 2013). A single-nucleotide polymorphism (SNP) is a variation in bases at

a single position in a DNA sequence among individuals and are frequently used for

determining kinship. (Syvanen 2001). Single-nucleotide polymorphism variants were

determined for each genome, a catalogue of all variants detected was made, and then

individuals were genotyped for the SNPs in the catalogue. Filtering of the data and

individuals was necessary to exclude outliers. Filtering was conducted using Plink v1.9

(Purcell et al. 2007, Heppenheimer et al. 2018). Plink is an open-source program that

allows for rapid analysis and manipulation of large genetics datasets (Purcell et al. 2007).

I applied strict filtering parameters for determining relatedness (Huisman 2017, vonHoldt

et al. 2020). Using Plink, I filtered to retain SNPs that had a minor allele frequency of 0.49 or less (--maf 0.49), had a missing genotype rate of 0.05 or greater (--geno 0.05), passed the Hardy-Weinberg equilibrium test with p-values ≤ 0.001 (--hwe 0.001), and excluded loci in statistical linkage disequilibrium using 3 parameters: a window size in variant count, a variant count to shift the window at the end of each step, and a pairwise r2 threshold (--indep-pariwise 50 5 0.2) (Purcell et al. 2007, vonHoldt et al. 2020).

I calculated pairwise relatedness of individuals in the filtered dataset using package "related" (Pew et al. 2015) in R (R Core Team 2020). Package "related" can provide relatedness coefficients calculated from seven different estimators: lynchli, lynchrd, quellergt, ritland, wang, dyadic likelihood estimator, and triadic likelihood estimator. A relatedness coefficient is an estimate of the probability that two individuals are related (Pew et al. 2015). There is no single relatedness estimator that is considered best in all situations, and the performance of the estimator often depends on the locus characteristics of a dataset. To determine which estimator to use on my dataset, I simulated 100 pairs of individuals for each degree of relatedness. These simulated pairs had known relationships and similar locus characteristics to my dataset. I then calculated correlation coefficients between observed and expected relatedness values for each relatedness estimator to allow for comparison of estimators. I used the relatedness estimator that resulted in the highest correlation coefficient. I used the coancestry function in package "related" to implement the relatedness estimator that performed best on the simulated data (vonHoldt et al. 2019). Relatedness coefficients range from 0-1 with values ranging from 0.43 - 0.57 indicating a first order relative (interpreted as full sibling or parent-offspring pair), values ranging from 0.13 - 0.34 indicating a second

order relative (interpreted as half sibling), values ranging from 0.11 – 0.12 indicating a third order relative (interpreted as extended family such as cousins), and values ≤ 0.10 indicating no relatedness.

Proximity Analysis

To quantify the proportion of time that males in a dyad spent within 50 m of each other, I calculated the weekly proximity rate for each dyad of males annually as:

Equation 1

$$Proximity\ rate = \frac{ST_{\alpha\beta}}{T_{\alpha\beta}}$$

Where $ST_{\alpha\beta}$ is the number of GPS locations simultaneous in space (< 50 m) and time (< 5 min) for wild turkeys α and β, and $T_{\alpha\beta}$ is the number of locations simultaneous in time (Long et al. 2014). The thresholds were determined based on GPS location error of 20 m and possible timing errors in GPS fix collection. The proximity rate was calculated using the wildlifeDI package (Long et al. 2014) in R (R Core Team 2020). Proximity rates approaching 1 indicate that the two turkeys spent the majority of their time within 50 m of each other. Proximity rates approaching 0 indicate that the two turkeys were rarely within 50 m of each other.

I classified each week as winter, mating, transition, or non-mating based on the season boundaries set from gobbling activity in each year. See Chapter 2 for details on gobbling analysis and season delineation. I used package ggplot2 (Wickham 2016) in R (R Core Team 2020) to visually examine the weekly proximity rates in relation to season and relatedness classification.

Results

I captured 10 males in 2020 in 4 flocks with flock size ranging from 2 - 3. I

captured 25 males in 2021 in 9 flocks with flock size ranging from 2-6. In 2020, one male

died prior to the end of the mating season and one male died during the summer non-

mating period. During 2021, 15 males either died or had transmitter malfunctions before

the end of the mating season and one male died during the summer non-mating period.

Blood samples were collected from all 35 adult males, and of these 35 adult males, DNA

for one male did not amplify during the analysis process, resulting in his exclusion from

DNA filtering and relatedness analysis, and one male captured in 2021 was a recapture

from 2020. This resulted in 33 adult male turkeys that were input into Plink for filtering.

Twenty-nine males passed through the Plink filters resulting in 400 SNP variants for

analysis in R. Nineteen males had both DNA data and GPS data through the mating

season. The data simulation and comparison of correlation coefficients recommended use

of the dyadic likelihood estimator to determine relatedness (dyadml; Milligan 2003) for

dyads in our data set (Table 3.1). I compared relatedness values for all possible dyads of

males in each year, resulting in relatedness estimates for 9 individual males in 72 dyads

for 2020 and 21 individual males in 420 dyads in 2021. The dyadml relatedness estimator

indicated that six dyads were first order relatives, three dyads were second order

relatives, and 5 dyads were third-order relatives. All other dyads showed dyadml

relatedness values that indicated that they were unrelated (Milligan 2003; Table 3.2).

One first order relative dyad (relatedness coefficient = 0.48) was captured in 2020

and were the only two males captured from a flock of three. The mean weekly proximity

value of this dyad across the entire 2020 study period was 0.84, as was the average

weekly proximity rate for the breeding season specifically (Figure 3.1). The weekly

proximity rate for this dyad never dropped below 0.70, indicating that ≥70% of simultaneous GPS fixes for the two males were within 50 m of each other. The second first order relative dyad (relatedness coefficient = 0.47) was captured in 2021 as part of a flock of 6 males. From this flock, I determined the two other pairs of birds, were unrelated and did not travel together during the study period. The mean weekly proximity rate of the first order relative birds for the entire study period was 0.17, and the mean weekly proximity rate for the breeding season specifically was .06 (Figure 3.2). Among all dyads, the pair that exhibited the highest mean weekly proximity rate (0.88) during the breeding season was captured together in 2021 and was unrelated. One of the males in this dyad died before the end of the study period, so I was only able to gather proximity data for the breeding season for this dyad (Figure 3.2). Three of the dyads that were first order relatives were not captured together as part of winter flocks and did not travel together during the study period.

Five winter flocks that were captured resulted in 7 dyads of unrelated males that I hypothesized would disperse from each other prior to the mating season. With the exception of two dyads, unrelated birds, captured together dispersed from each other prior to the mating season and were only observed together for a small proportion of time during the rest of the study period. As previously mentioned, one of these dyads of unrelated birds stayed together throughout the 2021 breeding season and exhibited the highest weekly proximity rate of all dyads. The second of these dyads broke up before the breeding season in 2020 but paired back up during the summer and exhibited high average weekly proximity rates (0.75; Figure 3.2).

Discussion

My hypothesis that males which traveled together during the breeding season would be siblings, was not fully supported. Of the six pairs of first-order relatives that I identified, only 3 were captured together in winter flocks. The other 3 pairs were trapped separately at trap sites that were several kilometers apart. The lack of movement data on these three pairs of birds makes it difficult to draw any conclusions, however they may provide evidence that the social structure of winter flocks on SRS is different than I originally assumed. While I only tracked movements of two dyads of first order relative males, the dyads exhibited contrasting behaviors. One dyad of first order relatives remained together during all seasons, whereas the other dyad of first order relatives separated prior to the breeding season and were rarely together during the remainder of the study period. Additionally, one pair of wild turkeys that traveled together during the breeding season were unrelated which contradicts my prediction that unrelated males would split up before the breeding season. There are several factors that could interfere with the interpretation of my data. My sample size was small, and it is possible that GPS tagged males may have also been traveling with males without GPS transmitters during the breeding season, so kin selection and cooperative courtship may have been occurring with an untagged male. The complex social and reproductive behaviors of wild turkeys also complicated my ability to assign sibling relationships to pairs of males. Although I could tell if dyads were related, I was unable to differentiate between different types of first and second order relatives based on relatedness coefficients, so my assumption that first and second order relatives are full and half siblings, respectively may not be entirely correct. Additionally, because males and females can each have multiple partners and females may engage in nest parasitism (Healy 1992), nest mates may not always be

related as has been previously assumed (Watts and Stokes 1971). Despite these possible complications, my results still cast doubt on the belief that the formation of sibling coalitions for cooperative courtship is ubiquitous across wild turkey populations (Healy 1992) and show there are likely differences between wild turkey population living in different habitats in terms of cooperative mating strategies and factors influencing this cooperation. My results also indicate that kin selection may not be the primary driver of cooperative courtship in wild turkeys.

The family Pipridae consists of over 50 species of manakins, small Neotropical passerines, many of which are known to participate in cooperative courtship, although, many variations in cooperation and courtship behaviors have been observed (DuVal 2007a, DuVal 2007b). Similar to wild turkey subspecies, there are variations in mating systems between manakin species. Some manakin species such as the long-tailed manakin (*Chiroxiphia* linearis; Foster 1977), are known to form leks similar to Rio Grande turkeys living in open habitats where multiple groups of male birds display in a common area, whereas other species such as the lance-tailed manakin (*Chiroxiphia lanceolata*) and the white-ruffed manakin (*Corapipo altera*) form exploded leks similar to eastern wild turkeys living in forested habitats (DuVal 2007b). While early research suggested that cooperative courtship was an obligate behavior for many manakin species (Foster 1977, DuVal 2007b), recent research has shown that cooperative courtship may be facultative behavior for lance-tailed manakins and white-ruffed manakins which use an exploded lek strategy (DuVal 2007b, Jones et al. 2014). Lance-tailed and white-ruffed manakins have been observed successfully mating as individuals as well as mating cooperatively (DuVal 2007b, Jones et al. 2014), indicating that individuals in the same

population, may choose whether or not to mate cooperatively depending on if cooperation appears to be advantageous. I believe that cooperative courtship may also be a facultative behavior for eastern wild turkeys on the Savannah River Site. Advantages of cooperative courtship may be a function of habitat. In order for a dominant male to prevent a subordinate male in a cooperating coalition from reproducing, he must have visual contact with the subordinate male. In heavily forested ecosystems, such as the Savannah River Site, heavy vegetation may obscure a dominant male turkey's view of nearby males, which could possibly influence a subordinate male's decision to cooperate or breed independently (Balph et al. 1980). If a solitary male turkey can successfully mate with any females, it may be more advantageous to mate as an individual rather than cooperating.

In wild turkeys, there has been evidence that kin selection may be responsible for cooperative courtship in some populations of Rio Grande turkeys (Watts and Stokes 1971, Krakauer 2005). Kin selection has been shown in other bird species that engage in cooperative courtship including black grouse (Hoglund et al. 1999), chestnut-crowned babblers (*Pomatostomus ruficeps*; Browning et al. 2012), and white-bearded manakins (*Manacus manacus*; Shorey et al. 2000), and has frequently been posited as a driver of cooperative courtship. However, individuals of several species of manakins participating in cooperative courtship have been unrelated, discounting the theory that kin selection is responsible for cooperative courtship in all cases (Foster 1977, McDonald and Potts 1994, DuVal 2007a, Loiselle et al. 2006). My results seem to follow a similar pattern as one pair of unrelated males remained together during the mating season. Like some manakin species, it is possible that other factors could be responsible for cooperative

courtship in eastern wild turkeys. In manakins, a delayed direct fitness benefit (increased

future mating opportunities) rather than an immediate indirect benefit (successful

reproduction of a relative) is thought to be a possible adaptive advantage of cooperative

courtship (DuVal 2007a). While subordinate males may not receive any indirect fitness

benefit form cooperative courtship, such is the case with kin selection, subordinate

cooperating males may directly benefit in the future. Several direct benefits have been

observed in manakins including eventual rise to dominant status (McDonald and Potts

1994, Duval 2007a) and taking advantage of female lek fidelity (McDonald and Potts

1994). Benefits not related to kin selection, such as rise to dominant status (McDonald

and Potts 1994, Duval 2007a) and greater protection from predators (Balph et al. 1980),

have not been studied in wild turkeys but may also provide an explanation of cooperative

courtship. If these benefits, outweigh the costs of attempting to reproduce on their own, a

male wild turkey may decide to participate in cooperative courtship.

While some pairs of related male wild turkeys may participate in cooperative

courtship and meet the qualifications of kin selection, it is possible that kin selection may

not be the only explanation for cooperative courtship in male wild turkeys. It is also

possible that participation in cooperative courtship is facultative and may be dependent

on other factors such as habitat type. The decision to breed cooperatively may be a

decision made by an individual based on perceived costs and benefits. Wild turkeys are a

good model species for trying to understand the fitness causes and consequences of

cooperative courtship, given the large range of ecosystems they inhabit and the variation

in mating strategies. More research incorporating direct measures of relatedness and

fitness benefits is necessary to better understand the degree to which cooperative

courtship and kin selection operate in different subspecies and habitats, and possibly

within single populations of wild turkeys.

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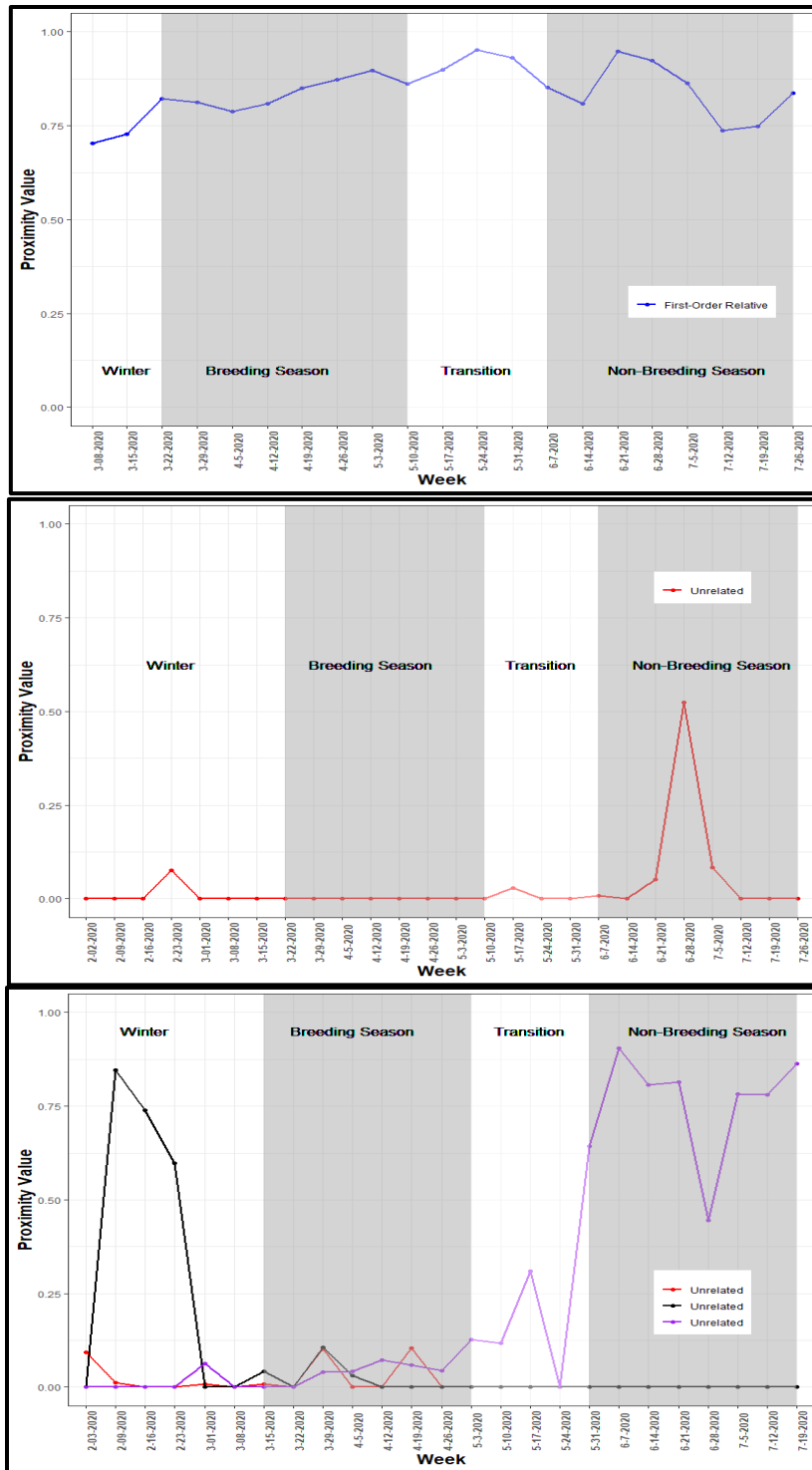Wittenberger, J.F. 1978. The evolution of mating systems in grouse. *The Condor* 80:126-137.

Tables and Figures

Table 3.1. Correlation coefficients between observed and expected values of 6 relatedness estimators used to assess relatedness of male wild turkeys captured on the Savannah River Site, South Carolina, 2020-2021. Expected values were based on 100 simulations derived from known data.

Relatedness Estimator	Correlation Coefficient
lynchli	**0.976**
lynchrd	**0.981**
quellergt	**0.981**
ritland	**0.975**
wang	**0.976**
dyadml	**0.987**

Table 3.2. Number of dyads of each relatedness category in flocks of adult male eastern wild turkeys captured on the Savannah River Site, South Carolina in 2020 and 2021.

Year	Total males captured	Pairs with known relatedness			
		1st Order	2nd Order	3rd Order	Unrelated
2020	2	1	-	-	-
	2	-	-	-	1
	3	-	-	-	3
	3	-	-	-	3
2021	4	-	-	-	6
	1	-	-	-	-
	1	-	-	-	-
	6	1	-	-	5
	3	-	-	-	3
	3	1	-	-	-
	2	-	-	-	1
	3	-	-	-	-
	2	-	-	-	1

Figure 3.1. Weekly proximity rates and relationships for winter flocks of adult male eastern wild turkeys captured together on the Savannah River Site, South Carolina in 2020. Only winter flocks for which GPS data was collected are shown. Each panel represents a different winter flock that was captured together, and different color lines represent different combinations of dyads from that flock.

Figure 3.2. Weekly proximity rates and relationships for winter flocks of adult male eastern wild turkeys captured together on the Savannah River Site, South Carolina in 2021. Only winter flocks for which GPS data was collected are shown. Each panel represents a different winter flock that was captured together, and different color lines represent different combinations of dyads from that flock.

4. Conclusions

The primary objective of this study was to provide data on the space use of male wild turkeys during the reproductive season without the confounding effects of hunting pressure. My results provided support for previous research that concluded that male wild turkeys increase their daily range size during the spring. Additionally, as hunting pressure was absent in my study, I was able to rule it out as a possible cause of changes in space use and conclude that reproductive behaviors of male wild turkeys are likely a major driver of increased movements during the spring. My results also showed, that in the majority of males, increased daily range size translates to increased seasonal range size, indicating that male wild turkeys do frequently expand the area they traverse during the mating season, likely in search of receptive females. My results indicate, that in the absence of hunting pressure, male wild turkeys can do what is necessary to maximize their reproductive success without having to consider if these decisions will negatively impact survival due to the increased risk of harvest. Continued research on the behaviors of wild turkeys in nonhunted populations is critical to understanding the spring behaviors of male wild turkeys.

Contrary to my predictions, my results indicated that male wild turkeys don't use space within their seasonal ranges differently between the mating and non-mating seasons. My results showed significant day-to-day variation in the way male wild turkeys use space within both seasons. The space use of male wild turkeys during the mating season was consistent with my prediction that there would be significant daily variation in space use due to fluctuating hormone levels in male turkeys during the reproductive season. However, my prediction that a focus of foraging rather than reproduction would lead to changes in the way turkeys use space was not supported and indicates that the

distribution of foraging resources or factors other than foraging resources may determine the movements and space use of male wild turkeys during the non-mating seasons. Future research focused on better understanding the resource priorities of male turkeys throughout the year may provide insight into the significant daily variation in space use patterns I observed during the non-mating season.

I sought to determine if male eastern wild turkeys living in a heavily forested ecosystem showed evidence of cooperative courtship and kin selection. My study had several limitations that made it difficult to draw conclusions about the prevalence of cooperative courtship and kin selection in eastern wild turkeys on the Savannah River Site. However, my results did cast doubt on the previous assumption that cooperative courtship and kin selection is ubiquitous across all turkey subspecies and habitats. While my study only had two pairs of birds that were first order relatives, they provided different results. One pair traveled together for the entire study period, which could indicate that kinship and cooperative courtship were operating in the population. The other pair never traveled together, indicating that cooperative courtship due to kin selection may not be present in the population. Another pair of completely unrelated birds stayed together for the entire breeding season, indicating that cooperative courtship may be operating, but kin selection may not explain the motivation behind cooperative courtship. From my results, it appears that cooperative courtship may be facultative in this population of wild turkeys and that kin selection may not fully explain the motivation behind cooperative courtship in all populations of wild turkeys. My results highlight the complexities of male wild turkey reproductive behaviors and show that mating strategies and the motivations behind these strategies are likely specific to site and individual. I

suggest further research across subspecies and habitat types that incorporates direct

measures of relatedness and reproductive success in order to determine factors affecting

the use of cooperative courtship.