Little is known about the ecology of mature (≥ 3-years-old) male white-tailed deer (Odocoileus virginianus), especially in forested landscapes with minimal human disturbance. I assessed spatial use, habitat selection, and breeding season movements of mature males in a northern hardwood forest in northern Pennsylvania. During December 2011 – April 2012, I equipped 19 mature males with GPS collars programmed to collect hourly fixes throughout the year as well as every 15 minutes from October through December. Home ranges of 15 study animals varied seasonally (fall $\bar{x} = 367 \pm 152$ ha; winter $\bar{x} = 334 \pm 40$ ha; spring $\bar{x} = 290 \pm 38$ ha; summer $\bar{x} = 168 \pm 25$ ha). Harvested stands and forest openings were important throughout the year. Acorn mast availability during late summer/fall prompted home range shifts to mature oak (Quercus spp.) stands. Mature males moved greater distances during the peak rut and daytime movements increased up to 8 times from pre-rut to rut period. Movement patterns were highly variable among bucks. Nine of the study animals engaged in infrequent, short-term, long-distance movements during spring.

INDEX WORDS: breeding season, excursions, GPS collars, habitat selection, home range, mature male, movements, northern hardwoods, Odocoileus virginianus, rut, spatial use, white-tailed deer
SPATIAL USE AND MOVEMENT ECOLOGY OF MATURE MALE WHITE-TAILED DEER IN NORTHCENTRAL PENNSYLVANIA

by

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B.S., The Pennsylvania State University, 2010

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CHAPTER 1
INTRODUCTION, LITERATURE REVIEW, OBJECTIVES, AND STUDY AREA

INTRODUCTION

Spatial use and movement ecology of white-tailed deer (*Odocoileus virginianus*) have received much attention in past research, but few of these studies have investigated mature (≥ 3 years old) buck movement ecology, partly because they typically represented a small portion of deer populations. Over the past 2 decades, however, management strategies that increase numbers of mature males (e.g., quality deer management) have become increasingly common (Adams et al. 2010). Of the studies done, most have been conducted using very high frequency (VHF) telemetry (Beier and McCullough 1990, Webb et al. 2007, Thayer 2009, Harrelson 2001, Walter et al. 2011). VHF telemetry typically permits only 1 or 2 locations per day and has relatively large associated telemetry error, which limits fine scale analysis of movement patterns or habitat use. While these studies certainly provided valuable insight into the spatial ecology of deer, analyses of data based on VHF telemetry are relatively coarse-scale. The recent development of global positioning system (GPS) collars allows researchers to collect fine scale data to evaluate space use and movement ecology of ungulates (Kochanny et al. 2009). Several recent studies have used GPS collars to investigate the movement ecology of female (Kolodzinski et al. 2010), male (Tomberlin 2007, Karns 2008, Foley 2012), or both sexes of deer (Webb et al. 2010, Basinger 2013). However, these studies occurred in either semiarid habitats or in areas which have significant anthropogenic influence such as agriculture, roadways, and...
developments. Movement studies conducted in semiarid habitats may have limited applicability in other regions and habitats. Further, home range and habitat use is undoubtedly influenced by anthropogenic impacts. To date, no studies have used GPS technology to investigate movement ecology and fine scale habitat use of mature bucks in areas of contiguous forest with minimal anthropogenic influences. Mature male behaviors in these conditions would likely reflect natural movements without significant influence of human disturbance.

Therefore, I used GPS collars to investigate the spatial ecology of mature, male deer in a lightly-exploited population occupying an unfragmented landscape on the Allegheny Plateau of northcentral Pennsylvania. Specifically, I evaluated seasonal home ranges and core areas, habitat selection, seasonal movement patterns, and breeding movements. Results of this research hold implications for understanding spatial use and movement ecology of mature male white-tailed deer under more natural settings than those areas with daily human activities by analysis of fine scale location and movement data. Results will also help develop guidelines for maximizing success of landscape management scale and strategies that attempt to increase representation of mature males in white-tailed deer populations.

**LITERATURE REVIEW**

Although the white-tailed deer is among the most researched wildlife animals in North America, much remains to be known about the movement ecology of mature males. Mature male movements change seasonally related to seasonal variations in climate, forage availability, and reproductive or social activities. During spring and summer males often form bachelor groups consisting of 2 or 3 adults and several yearlings, and membership in bachelor groups may vary through the spring and summer (Hirth 1977). Changing photoperiod in the fall results in rising testosterone levels which results in antler calcification and velvet shedding. The increase
of testosterone levels also causes social intolerance among members of bachelor groups as breeding season approaches, resulting in the breakup of these small groups (DeYoung and Miller 2011). Following the breeding season, testosterone concentrations decline and bucks reform bachelor groups during the late winter or early spring.

Seasonal changes in forage availability and changing nutritional requirements may also impact habitat use and movement patterns of mature males (DeYoung and Miller 2011). During spring and summer, high forage availability often results in reduced movements and smaller home ranges of mature males compared to other seasons (Tomberlin 2007). During fall, energy requirements cause a shift to high energy foods due to demands for lipogenesis in preparation for the breeding season and subsequent winter. Acorns, fruits, other hard and soft mast, and agricultural crops are important energy sources. In fact, hard mast such as acorns may account for as much as 76-90% of a whitetail’s diet during the fall when available (Harlow et al. 1975, McCullough 1985). Deer habitat use will reflect this availability of high energy food sources as deer concentrate on habitats such as mature hardwoods or agricultural fields (McCullough 1985, Tomberlin 2007).

Prior to European colonization, white-tailed deer herds had an older age structure and lower population turnover compared to contemporary deer populations (Elder 1965). Primeval hunters apparently avoided harvesting fawns, and harvested a greater portion of mature (> 6.5 years old) deer than contemporary hunters. However, during the last 20 to 30 years, management strategies have slowly shifted from the heavy male exploitation strategies common during the population restoration phase (Adams and Hamilton 2011) to an increased popularity of selective harvest guidelines such as quality deer management. As a result, harvest rates of fawn and yearling males have declined in most regions of the country (Adams et al. 2009).
Nationwide yearling buck harvest has declined from 51% of the adult male harvest in 1999 to 45% in 2005 (Adams et al. 2009). For example, after the Pennsylvania Game Commission adopted antler restrictions in 2002 (Pennsylvania Game Commission 2009), yearling male harvest rates dropped from 80% in 1999 to 52% in 2005 (Adams et al. 2009). Antler restrictions and lower harvest rates of yearling males have resulted in an increased frequency of mature males in many populations. Understanding how mature males use the landscape will help managers develop efficient and effective management plans.

Previous investigations of white-tailed deer spatial ecology using VHF technology reveal that home range utilization will shift seasonally depending on food availability and weather conditions, such as snow depth in the northern regions (Tierson et al. 1985, Beier and McCullough 1990, Brinkman et al. 2005). Spring and summer ranges typically are smaller than during other seasons, likely due to greater food availability (Beier and McCullough 1990, Hellickson et al. 2008). During fall male white-tailed deer expand their home range (Nelson and Mech 1981, Kammermeyer and Marchinton 1977), a behavior attributed to breeding activities (Beier and McCullough, 1990). However, this increase in home range size during autumn has not been reported in all studies (see Hellickson et al. 2008). In northern regions where yarding occurs during deep snow conditions, winter home ranges shrink significantly due to the metabolic cost of travel and activity (Nelson and Mech 1981, Tierson et al. 1985). However, Brinkman et al. (2005) reported an increase of winter home range in an area with intense agricultural availability in southwestern Minnesota.

The availability of GPS technology has allowed acquisition of finer scale data on seasonal home range sizes and shifts, response of deer to hunter pressure, and breeding season movements of mature bucks and does. In one of the first studies using GPS technology to
investigate movements of mature bucks, Tomberlin (2007) reported that home ranges were smallest during summer and largest during the fall in an agricultural setting in Maryland. He also observed home range shifts from summer to winter with the changes in forage availability and cover. In a subsequent study on the same area, home range size did not change as a result of hunting pressure (Karns 2008). Study animals were not pushed outside of their home range and normal behaviors resumed just hours after disturbance from a hunter. A subsequent study that focused on response to hunter pressure indicated that mature males respond to high hunter density (1 hunter/30 ha) by decreasing linear movements and increasing tortuous movements in smaller areas (Little 2011). Mature males also altered resource selection by seeking security cover, higher elevations, gentle slopes, and areas away from roadways when exposed to human predation risk (Little 2011).

GPS technology has also allowed the identification and description of temporary excursions outside of established home ranges during the breeding season (Tomberlin 2007, Karns et al. 2011, and Foley 2012). Reasons behind these movements likely are related to breeding behavior as males may venture outside of their home range in pursuit of a receptive female or to isolate a female from other male competition (Hirth 1977). These excursions are important to managers as they may affect harvest vulnerability by venturing into areas with higher hunter densities.

Other fine scale movements of males during the breeding season have been investigated via GPS technology. As previously identified from studies using VHF technology, GPS-based studies confirm that mature male movements increase during the fall breeding season (Tomberlin 2007; Hellickson et al. 2008; Karns 2008; Webb et al. 2007, 2010; Little 2011; Foley 2012; Basinger 2013). With increased movements, previous research has also found bucks to increase
home range size, which is thought to be a breeding-related behavior as it increases chances of males encountering receptive females (Nelson and Mech 1984, Beier and McCullough 1990, Tomberlin 2007). However, more recent studies indicate that breeding activities of mature males are sometimes restricted to previously established home ranges (Hellickson et al. 2008, Webb et al. 2010, Little 2011). Confined home ranges during the breeding season and high home range fidelity may provide protection and security to some individuals (Hellickson et al. 2008, Webb et al. 2007). Foley (2012) even noted a decrease in home range size in some males associated with an increase in mate-search intensity. In contrast, Webb et al. (2010) found that movements were 20% greater during rut than post-rut and these movements were more linear, indicating that males were actively seeking or pursuing females in estrus.

The advent of GPS technology has also allowed detailed investigations of mate searching behaviors by mature males. Tomberlin (2007), Webb et al. (2010), and Basinger (2013) observed that males employed the dominant floater behavior as described by Brown (1974), where males covered large portions of their home range with continuous movement and returned to the point of origin within 30 hours. Foley (2012) describes the Levy walk, which consists of short steps scattered with long step lengths; and Brownian movements which consist of constant short-step lengths that follow an exponential distribution. In that study, most adult (≥ 3 years old) males demonstrated the Brownian movements, while younger (≤ 2 years old) males demonstrated the Levy walk behavior and lower search intensity. Younger males appeared to invest less effort in searching for females, suggesting that they take on the strategy of opportunistically pursuing females when possible. This suggests that males invest greatest search effort when physical maturity (3 years old) is reached (Foley 2012).
To date, all studies using GPS technology to describe the spatial and movement ecology of mature male whitetails have been conducted either in semi-arid environments or in highly fragmented landscapes such as agricultural areas. However, home ranges, habitat selection, and breeding season movements of mature males in areas of contiguous forest with limited anthropogenic influence such as only hunting activities have not been adequately described. Therefore, I used GPS collars to investigate the spatial ecology of mature, male deer in a lightly-exploited population occupying an unfragmented landscape on the Allegheny Plateau of northcentral Pennsylvania. This research specifically adds to the knowledge of how mature males naturally navigate their landscape and habitats where human influences are minimal. As the proportion of mature males increases in Pennsylvania’s deer herds due to changes in harvest guidelines introduced by the Pennsylvania Game Commission in 2002, it is important for managers to understand how these animals are using the landscape and habitats when managing populations, harvest rates, and potentially the spread of disease (Webb et al. 2007, Hellickson et al. 2008).

OBJECTIVES

The goal of my research was to study the spatial and movement ecology of mature (≥3.5 years) male white-tailed deer in a forested landscape in northcentral Pennsylvania. My specific objectives were to: (1) examine differences in home range, core area, and habitat selection among seasons and between hunted versus non-hunted periods within a season; and (2) compare fine-scale temporal movements during breeding and hunting seasons.

STUDY AREA

Capture activities were conducted on an approximately 3,000-ha tract of privately owned land, managed under strict quality deer management guidelines, such as only harvesting males ≥
4 years old and an established food plot program; located in northcentral Pennsylvania. The entire study area (~6,700 ha) was defined by creating a minimum convex polygon with a 200-meter buffer around all mature buck locations, excluding notable short-interval long distance excursions. The study area focused on the private land where capture activities occurred but included adjacent state-owned and privately owned lands. The study site lies on the Allegheny Plateau and elevations ranged from approximately 430-670 m. The habitat of the study area was primarily contiguous forest, consisting of mostly mature and regenerating northern hardwood forest species including oaks (*Quercus* spp.), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), eastern hemlock (*Tsuga canadensis*), ash (*Fraxinus* spp.), cucumber magnolia (*Magnolia acuminata*), and tulip poplar (*Liriodendron tulipifera*). Small forest openings were also present (1.0% of study area), and contained fescue grass (*Festuca* spp.) or agronomic crops planted to supplement native deer forage such as clover (*Trifolium* spp.), forage chicory (*Chicorium intybus*), and brassicas (*Brassica* spp.). Supplemental protein feeding occurred throughout the privately owned land during the winter months. Human disturbance on the area consists of only periodic road and food plot maintenance. Hunting pressure is light, consisting of approximately 5 hunter-days /week during the 6 week archery season, and 18 hunter-days /week during the 2-week firearms season.
LITERATURE CITED


CHAPTER 2

SEASONAL HOME RANGES AND HABITAT SELECTION OF MATURE MALE WHITE-TAILED DEER IN NORTHERN PENNSYLVANIA

ABSTRACT

Although the use of global positioning system (GPS) collars has provided new insights into deer spatial ecology, relatively little is known about this topic as it relates to mature (≥ 3-years-old) male white-tailed deer (Odocoileus virginianus), especially in unfragmented landscapes where human disturbance is minimal. Therefore, we studied spatial use and habitat selection of mature males in a forested landscape on the Allegheny Plateau of northern Pennsylvania. During December 2011 – April 2012 and July 2012, we fit mature male deer with GPS collars programmed to collect hourly fixes. Upon collar retrieval, we had sufficient data to assess seasonal home ranges, core areas, and habitat selection for 15 deer during ≥1 season. Home ranges varied seasonally ($P = 0.04$) and were larger during fall ($\bar{X} = 367 \pm 152$ ha) and winter ($\bar{X} = 334 \pm 40$ ha) than summer ($\bar{X} = 168 \pm 25$ ha). Although habitat selection within home ranges varied seasonally, select-harvested and clear-cut stands ($P< 0.001$), as well as forest openings ($P< 0.001$), were important throughout the year. Forest openings ($P = 0.069$) were also an important component of core areas. Onset of mast drop during late summer/fall prompted home range shifts to stands of mature oaks. Our results indicate that early successional areas are an important habitat requirement of mature males in northern hardwood forests as they were used disproportionately to their availability. However, seasonal changes in home range and core area sizes highlight the importance of habitat diversity as well as landscape-scale management of forest communities in northern hardwood regions.

INDEX WORDS: GPS collars, habitat selection, home range, mature male, northern hardwoods, spatial use, white-tailed deer
INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) are the most sought after game species in the United States, and hunters spent $18.1 billion on deer hunting during 2011 (Southwick Associates 2012). In addition to their economic value, as selective browsers, deer can shape the development of regenerating forests, and are considered a keystone herbivore (Waller and Alverson 1997). Thus, numerous studies have assessed white-tailed deer spatial ecology. However, disproportionate research has focused on adult and juvenile females, as well as juvenile (≤ 2.5 years old) males. In contrast, relatively little is known about season-specific habitat selection or home ranges of mature (≥3.5 years old) males, probably because this sex-age class has traditionally comprised a very small segment of deer populations. However, recent changes in antlered male harvest regimes at the state or local level have resulted in increasing representation of mature males in deer populations. For example, after the Pennsylvania Game Commission adopted antler restrictions in 2002 (Pennsylvania Game Commission 2009), yearling buck harvest rates dropped from 80% in 1999 to 52% in 2005 (Adams et al. 2009).

The spatial distribution of the few studies investigating spatial ecology of mature male deer is geographically confined to areas of Texas (Webb et al. 2007, 2010, Hellickson et al. 2008, Foley 2012), Louisiana (Thayer 2009, Harrelson 2011), Maryland (Tomberlin 2007, Karns 2008), or New York (Tierson et al. 1985). Mature male home ranges in an agricultural area of Maryland were smallest during summer, probably a result of increased forage availability via row crops, and largest in fall, likely due to breeding activities (Tomberlin 2007). In this area, home ranges shifted seasonally in response to changes in forage and cover availability as crops were harvested. On the same study area, Karns (2008) reported that home range and core area size of mature males during the breeding and hunting seasons did not vary during the pre-hunt,
hunt, and post-hunt periods. Similarly, in the mesquite (*Prosopis glandulosa*) scrub-bush region of southern Texas, home ranges of mature males were larger during the breeding season (Webb et al. 2007, 2010). Interestingly, males ≥ 3-years-old had smaller home ranges and core areas than males ≤ 2-years-old. However, this increase in home range size during autumn has not been reported in all studies. For example Hellickson et al. (2008) reported that home ranges of adult males did not expand during the breeding season, but core areas did shift, suggesting a response to variation in availability of receptive females within previously established home ranges.

In a more recent study in an agriculture and cattle production landscape in southern Texas, Foley (2012) found that home range size decreased during the peak rut, suggesting that bucks focused their mating activities on specific portions of their home range. Webb et al. (2008) similarly investigated the effects of supplemental feed sites on home ranges and spatial distribution of adult males in the scrub-bush region of southern Texas. They reported that permanent supplemental feed sites did not appear to affect home range location, but rather influenced the size and shape of the range.

Home ranges have been reported to shift around the landscape as food availability changes seasonally (Kie et al. 2003, Bowyer and Kie 2006, Stewart et al. 2011) and have been reported in northern deer herds (Heezen and Tester 1967, Rongstand and Tester 1969, Sparrowe and Springer 1970, Tierson et al. 1985). Tierson et al. (1985) reported a shift in center of activity of adult male home ranges during the breeding season, presumably to increase number of doe interactions. They also reported a winter-summer shift associated with snow depths and timber harvest locations, where winter ranges were smaller than summer ranges. Tomberlin (2007) found in an agriculture landscape that home ranges of bucks also shifted from summer to winter, most likely due to changes in forage and cover availability as crops were harvested. Although
males primarily used cropland habitats during summer and woodland habitats during fall and winter, cropland and grassland were used throughout the year.

Although the results of these studies are informative, their applicability to other areas may be limited by the unique characteristics of the landscapes where they were conducted. The nutritional and behavioral ecology of deer in the mesquite (*Prosopis glandulosa*) scrub-bush region of southern Texas may differ from other regions (Hirth 1977). Similarly, anthropogenic influences on study areas, such as agricultural development, roadways and human development may impact deer movements and home range size (Storm et al. 2007, Grovenburg et al. 2009).

Therefore, because of the combination of increased management for mature males and the relative lack of information on their spatial ecology, our objective was to improve understanding of seasonal home range sizes and habitat selection of mature males in a relatively unfragmented, heavily forested, mountainous landscape in northern Pennsylvania. Anthropogenic influences in this region were minimal, as they consisted of only hunting and periodic road and food plot maintenance; and food availability likely was more limited seasonally than in the south Texas scrub-bush region or in agricultural landscapes.

**STUDY AREA**

We captured mature male deer (≥ 3.5 years-old) on an approximately 3,000-ha tract of privately owned land in northcentral Pennsylvania. The entire study area (~6,700 ha) was defined by creating a minimum convex polygon, with a 200-m buffer, around all mature male locations, excluding notable short-interval, long-distance excursions. The study area was centered on the private land where capture activities occurred but also included adjacent state- and privately-owned lands (Figure 2.1).
The area was located within the Allegheny Plateau region of Elk County, PA, and elevations ranged from approximately 430-670 m. The habitat was primarily contiguous forest, consisting mostly of mature or selectively harvested/clearcut northern hardwoods including oaks (Quercus spp.), black cherry (Prunus serotina), American beech (Fagus grandifolia), red maple (Acer rubrum), sugar maple (A. saccharum), American basswood (Tilia americana), yellow birch (Betula alleghaniensis), sweet birch (B. lenta), eastern hemlock (Tsuga canadensis), ash (Fraxinus spp.), cucumber magnolia (Magnolia acuminata), and tulip poplar (Liriodendron tulipifera). Timber harvesting on portions of the study area occurred from the 1990’s to 2005. Residual basal areas ranged from 0 to approximately 50 square feet/acre, which resulted in a dense herbaceous and woody understory across all harvested areas. In contrast, understory vegetation in the areas of mature forest was sparse and consisted primarily of hay-scented fern (Dennstaedtia punctilobula), New York fern (Thelypteris noveboracensis), and mountain laurel (Kalmia latifolia). Small forest openings were also present (1% of the study area), and contained fescue grass (Festuca spp.) or agronomic crops planted to supplement native deer forage such as clover (Trifolium spp.), forage chicory (Chicorium intybus), and brassicas (Brassica spp.).

Supplemental protein feeding occurred throughout the privately owned land during winter months. Human disturbance on the area consists of only periodic road and food plot maintenance. Hunting pressure is light, consisting of approximately 5 hunter-days /week during the 6 week archery season, and 18 hunter-days /week during the 2-week firearms season.

METHODS

Deer Capture and Handling

We equipped 15 mature (≥ 2.5 years old) male deer with global positioning system (GPS)-enabled collars from 15 December 2011 to April 2012. We deployed 3 Lotek 3300L
(Lotek Wireless Inc., Newmarket, Ontario, Canada) and 12 Followit Tellus® 5H1D (Followit AB, Lindesberg, Sweden) collars.

We captured deer using a combination of free-darting, rocket nets, and clover traps. When free-darting, we used 3-ml transmitter darts (Pneu-dart Inc., Williamsport, PA) to intramuscularly inject a Telazol® (Fort Dodge Animal Health, Fort Dodge, IA)/xylazine hydrochloride (Congaree Veterinary Pharmacy, Cayce, SC) (480mg/315mg) mixture to immobilize deer. We immobilized mature males captured in rocket nets and clover traps with an intramuscular Telazol®/xylazine hydrochloride (240mg/180mg) injection. To reduce recovery time in cold temperatures (< -6ºC) we changed immobilization for bucks captured in rocket nets and clover traps to 2 ml xylazine hydrochloride (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA). During immobilization, we monitored vital signs, treated for any minor injuries, lubricated eyes, and blindfolded each deer.

While immobilized, each mature buck was equipped with a GPS collar, tightened within 8 cm (approximately 4 fingers width) of the deer’s neck to allow for next swelling associated with the breeding season. We estimated deer age using tooth replacement and wear characteristics (Severinghaus 1949). During data collection, all males were ≥ 3-years-old. Live weight was estimated from chest circumference measurements (Pennsylvania Game Commission), and the date and location of each capture was recorded. Each deer also received colored and numbered ear tags (National Band and Tag Co., Newport, KY, USA) to allow for remote visual identification. Following processing, all deer that were injected with Telazol®/xylazine hydrochloride mixture received 3 ml of Tolazoline HCl (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA) as an antagonist, administered half intramuscularly and half intravenously, 80 minutes after immobilization injection. Deer immobilized with only xylazine
were reversed with 3 ml of Tolazoline HCl, administered half intramuscularly and half intravenously immediately after all data were recorded. All deer were monitored until fully mobile. Animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (#A2011-08-025-Y1-A0). Deer capture activities were approved by the Pennsylvania Game Commission and conducted under Special Use Permit No. 184-2011.

Data Collection and Monitoring

All mature males were fitted with mortality sensitive GPS collars programmed to record hourly fixes throughout deployment. We monitored deer 1 time/week using VHF-telemetry equipment to ensure study animals were alive and that collars were functioning properly. If a mortality or failure signal was detected, the collar was retrieved immediately using radio telemetry. At the end of the study, activation of a remote-release mechanism or a timed release mechanism was used for retrieval of the collars from the field.

Upon collar retrieval, we used the Lotek GPS 3000 Host Application (Lotek Wireless Inc., Newmarket, Ontario, Canada) and the Followit Tellus TPM Project Manager (Followit AB, Lindesberg, Sweden) software to download positioning data. To decrease the probability of erroneous points in the datasets, non-fix and impossible locations were censored from the dataset. After data censoring, we imported GPS fixes for each deer into ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) and projected them in Universal Transverse Mercator (UTM) North American Datum (NAD) 1983 Zone 17N (meters). Collar location error (18 meters) was measured by taking mortality events from 4 collars distributed throughout the study area and obtaining the mean X and Y position from 100 random points during the mortality event (stationary collar). The mean position was then plotted in ArcMap.
and the “point distance” tool in ArcToolbox (Environmental Systems Research Institute, Inc., Redlands, CA) was used to obtain mean distance from GPS locations to mean mortality location.

**Data Analysis**

We used the hourly fixes to construct seasonal home ranges and core areas. We constructed 95% home ranges and 50% core areas using the Dynamic Brownian Bridge Movement Model (hereafter, DBBMM; Kranstauber et al. 2012) Package for the R software version 3.0.0 (R Development Core Team 2013). Briefly, this model converts point locations to movement paths and uses them to construct utilization distributions. The DBBMM works well with intensively-sampled GPS tracks that include failed or missing fixes. The model uses likelihood statistics to determine change points along an animal’s movement path, and creates a measure of movement-based behavioral changes. In contrast to the original Brownian Bridge Movement Model (Horne et al. 2007), the DBBMM allows the variance of Brownian motion to fluctuate along the movement path, creating a more refined utilization distribution (Kranstauber et al. 2012). We selected model objects, margin and window size as suggested by Kranstauber et al. (2012) and Byrne et al. (2014).

We defined the seasons based from the astronomical calendar but still remaining biologically meaningful to male white-tailed deer. Spring was from 20 March-20 June, when snow cover receded and green-up began. Summer was from 21 June-5 September and coincided with peak forage availability during which males were adding both body and antler mass in preparation for the rigors of breeding. Fall was from 6 September-20 December, and covered the period from just after velvet shedding through the breeding season, as well as the peak drop of hard and soft masts. Winter was from 21 December-19 March, when deer were recovering from
breeding season, food was limited, and snow cover was greatest. We also created composite
home ranges and core areas for each individual using data from all seasons.

We delineated habitat types within the study area using aerial imagery and ground
verification. Habitat types included select harvest timber, clearcut timber, mature timber,
evergreens, and forest openings. We defined select harvest timber stands as those where saw
grade timber was removed ≤ 12 years prior. Clearcut stands were defined as those where all
trees were removed ≤ 10 years prior. We combined select harvest stands and clearcut stands for
habitat analysis because of the resulting dense herbaceous and woody understory vegetation
growth in both clearcuts and selectively harvested areas, and the removal of virtually all mature
mast-bearing trees in the select cuts. Forest openings consisted of fallow fields, fescue grass
openings, and food plots specifically planted with agronomic crops such as clover, forage
chicory, and/or brassicas. Evergreens were dense stands of eastern hemlock with very little
understory, primarily occurring on upper north facing slopes or along riparian areas.

We intersected home ranges, core areas, and point locations with the delineated habitat
types. We calculated habitat availability within the study area, home ranges, and core areas
using the command isectpolyrst in the software program Geospatial Modelling Environment
version 0.7.2.0 (Beyer 2012) to obtain the percent of each habitat type within a polygon. We
then used compositional analysis (Aebischer et al. 1993) to determine season-specific habitat
selection at 3 spatial scales; home range versus the study area (1st order), core area versus home
range (2nd order), and point locations versus home range (3rd order, Chamberlain et al. 2003).

Compositional analysis uses log-ratios of habitat use and, thus, becomes problematic
when there are values of zero use. To address this issue, when a habitat type was not represented
in a male’s space use at a given scale, we substituted a value of 0.7, as suggested by Bingham
and Brennan (2004), to minimize the risk of type I error. We examined the significance of habitat selection using the Wilkes lambda test (Aebischer et al. 1993). If significant differences existed between habitat availability and selection at a particular spatial scale, we created a ranking matrix of t-tests to assess the order of habitat selection during each season.

RESULTS

During the 2012 hunting season, 4 collared males were harvested by hunters. The mortality cause for an additional male, which died 2 weeks prior to initiation of the hunting season, was unknown. Nine collars (60%) ceased functioning at various times during the study period; thus sample sizes were uneven among seasons (Table 2.1). Collar location error was calculated to be 18 m.

We calculated seasonal home ranges and core areas for 15 adult males during 21 December 2011 – 20 December 2012 (spring, n = 13; summer, n = 10; fall n = 3; winter, n = 14). Home range size differed among seasons (F3, 36 = 3.17, P = 0.04) and was largest during fall and smallest during summer (Table 2.1). Core area size also differed among seasons (F3, 36 = 3.20, P = 0.03) and was largest during winter, and smallest during summer. Mean composite home range and core area size were 403 ha (SE = 37) and 58 ha (SE = 6.1), respectively.

The study area was comprised of 63% select harvest/clear cut timber, 29% mature timber, 7% evergreen forest, and 1% forest openings. We excluded the fall season from statistical analysis of habitat selection due to small (n = 3) sample size. Habitat selection varied seasonally and according to the scale of selection (Table 2.2).

Deer home ranges contained disproportionately more select harvest/clearcut timber than was available in the study area (1st order selection) during spring (λ= 0.216, P < 0.001), summer (λ = 0.137, P< 0.001), and winter (λ= 0.008, P< 0.001). Forest openings were the second most
selected habitat type during summer and winter, while evergreen habitat was second most selected in the spring (Table 2.2).

Core areas contained disproportionately more forest opening habitat than was available in the home range (2nd order of selection) during the spring ($\lambda= 0.580, P = 0.07$). Select harvest/clearcut timber was the second most selected habitat type during this season. In contrast, mature timber was most selected during the winter ($\lambda= 0.227, P < 0.001$), followed by forest openings. There was no difference in selection of habitat types during the summer ($\lambda= 0.719, P = 0.33$) at the 2nd order of selection.

Point locations were located within forest openings disproportionately to their availability within the home range (3rd order of selection) during spring ($\lambda= 0.415, P = 0.001$) and winter ($\lambda= 0.292, P = 0.001$). Select harvest/clearcut timber and evergreens were the second most selected habitat types during spring and winter, respectively. There was no difference in habitat selection during the summer season ($\lambda= 0.796, P = 0.516$) at this scale.

Although the sample size for the fall season limited statistical inferences, evergreens and select harvest/clear cut timber, mature timber, and forest openings were the most preferred habitat types at the 1st, 2nd, and 3rd order levels of selection, respectively.

Differences in habitat selection among seasons and spatial scales led to seasonal shifts in home range locations for several deer. Specifically, for the 3 males with available home range data during fall, all demonstrated a home range and/or core area shift from summer to fall. Clover/chicory food plots appeared to influence spatial use during spring and summer, while areas containing mast-producing hardwoods influenced spatial use during late summer and fall. For example, 2 males (#1 and #5), who frequently traveled together, used mature timber in the same area from 30 August until the third week of October (Figures 2.2 and 2.3). The third male
began frequenting a small area of mast producing oaks from 4 September until the fourth week of October. He then returned to the same oak stand during the third week of November, presumably following the conclusion of breeding activities, and continued to frequent the stand throughout December (Figure 2.4).

**DISCUSSION**

**Home Range**

We predicted that mature males would have larger home ranges than those in previous studies due to fewer anthropogenic barriers; such as roadways, fence rows, and developments. However, the average composite home range of mature males in our study was 404 ha ($SE = 36.5$ ha) in size, and was very similar to that reported in the mesquite scrub-bush region of southern Texas (Webb et al. 2010, Hellickson et al. 2008). Similar mean annual home ranges have been reported in an agricultural area of Maryland (Karns 2008), although Tomberlin (2007) observed smaller annual home ranges on the same study area.

Home range size decreased from spring to summer, and then increased markedly during fall and winter. Spring home range size, $290 \pm 38$ ha, was similar to what was reported in north Louisiana, $231 \pm 145$ ha (Harrelson 2011). The average summer home range size of deer in our study ($168 \pm 25$ ha) was similar to that of $233 \pm 23$ ha in New York (Tierson et al. 1985) and 115 ha in Maryland (Tomberlin 2007). Although limited by sample size, fall home range size ($367 \pm 152$ ha) was also similar to that reported for deer in Maryland, $299 \pm 31$ ha and $386 \pm 129$ ha, (Tomberlin 2007, Karns 2008) and Texas, $389 \pm 58$ ha (Webb et al. 2010). While our study area was minimally influenced by anthropogenic factors, mature males maintained home ranges similar in size to those reported in other habitats or in regions with more human influence. Thus,
annual home range size may only marginally be affected by landscape features, and values reported in the literature may reflect behavioral limitations.

We observed a seasonal pattern in home range size similar to that previously reported. Home ranges were smallest during summer, at a time when forage quality and quantity is greatest. Additionally, maternal aggression from females rearing fawns may restrict male movements (Ozoga et al. 1982). Home ranges expanded during fall resulting from breeding-related movements as males attempted to increase the probability of encountering a receptive female by expanding their range (Nelson and Mech 1981, Beier and McCullough 1990). The deer in our study continued to cover relatively large areas during winter, probably as a result of a mild winter with below average snow depths that did not restrict deer movements. Observations of deer yarding during winter months did not occur.

Seasonal shifts in home ranges have been reported elsewhere for northern deer (Heezen and Tester 1967, Rongstand and Tester 1969, Sparrowe and Springer 1970). As we observed, mast such as acorns can affect fall space use as deer will travel to locations harboring abundant acorns (McShea and Schwede 1993). Acorns and other hard mast species serve a vital role in accumulation of fat deposits for survival during the winter months (Mautz 1978, McShea and Schwede 1993). The deer in our study that did not shift their home ranges to incorporate mast crops appeared to compensate by including forest openings in their home ranges and frequenting these areas often. However, 3 males had home ranges that did not include food plots and these deer maintained similar home ranges across seasons. Supplemental protein feeders were present throughout the private land of the study area during the winter months, and these sites were within the winter home ranges or in close vicinity. Webb et al. (2008) reported that
supplemental protein feeders alone do not influence deer spatial use, but rather many other habitat components may have a stronger influence.

**Habitat Selection**

Select harvest/clearcut timber was the most available habitat type on the study area, yet was the most selected habitat during spring, summer and winter at the 1st order level of selection. Decreased canopy coverage following partial or complete canopy removal released a variety of plants preferred or moderately preferred by deer including blackberry (*Rubus alleghaniensis*), elderberry (*Sambucus canadensis*), viburnums (*Viburnum* spp.), wild grape (*Vitis* spp.), greenbrier (*Smilax* spp), hardwood seedlings, and a variety of annual and perennial herbaceous plants.

Although forest openings accounted for only 1.09% of available habitat within the study area, they were important at both the 2nd and 3rd orders of selection. Many of these openings were planted in deer-specific forage species such as clovers and forage chicory, which are high in protein and help deer meet the nutritional demand of body and antler growth during spring and summer, and brassicas which are easily digestible and high in energy, particularly during the winter when other food sources are less abundant and/or digestible.

Mature timber was the highest ranking habitat type during winter at the 2nd order of selection, indicating that it was an important component of winter core areas. The hard mast produced by some mature hardwood species such as oaks, is high in fats and carbohydrates and provides the energy critical to winter survival. Evergreen stands provide thermal cover and reduce snow depth and, when interspersed throughout mature hardwood stands, benefit deer by creating thermal and bedding cover in close proximity to hard mast.
Management Implications

Our results are indicative of the importance of both scale and diversity in managing deer in Northeastern climates with the goal of increasing representation of mature males in the herd. For example, deer home ranges in our study were, on average, over 400 ha throughout the year, much larger than a typical private landholding. Therefore, collaboration among landowners is crucial to successfully managing for mature males (Webb et al. 2007). In the northern hardwoods landscape we studied, habitat diversity is often limited and large tracts of continuous mature forest are common. Forest management to intersperse successional and mature forest habitats throughout the landscape will likely enhance habitat quality by providing preferred seasonal habitats. Forest openings planted with deer-preferred forage that can augment other forages can likely provide seasonal benefits.
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Produced for the National Shooting Sports Foundation in partnership with the

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Table 2.1. Mean seasonal and composite 95% home range and 50% core area size (ha) created using the Dynamic Brownian Bridge Movement Model plus associated standard errors from GPS collared mature (≥ 3 years old) bucks in northcentral Pennsylvania from December 2011 – December 2012.

<table>
<thead>
<tr>
<th>Season</th>
<th>n (home ranges)</th>
<th>HR ± SE</th>
<th>CA ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>13</td>
<td>290.2 ± 38.2</td>
<td>44.0 ± 6.3</td>
</tr>
<tr>
<td>Summer</td>
<td>10</td>
<td>167.9 ± 25.0</td>
<td>24.2 ± 3.9</td>
</tr>
<tr>
<td>Fall</td>
<td>3</td>
<td>367.1 ± 152.4</td>
<td>47.0 ± 16.0</td>
</tr>
<tr>
<td>Winter</td>
<td>14</td>
<td>334.3 ± 40.4</td>
<td>46.7 ± 4.6</td>
</tr>
<tr>
<td>Composite*</td>
<td>15</td>
<td>403.7 ± 36.5</td>
<td>57.5 ± 6.1</td>
</tr>
</tbody>
</table>


*Home range and core area for all seasons that data was collected on individual bucks
### Table 2.2

Seasonal ranks (0 = lowest, 3 = highest) of habitat selection across three spatial scales (habitat selection in home ranges vs. habitat availability across study area [1st order], habitat selection in core use areas vs. habitat availability in home ranges [2nd order], and habitat used vs. habitat availability across home ranges [3rd order]) based on compositional analysis of mature (≥ 3 years old) male white-tailed deer in northcentral Pennsylvania from December 2011 – December 2012.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>1st order selection</th>
<th>2nd order selection</th>
<th>3rd order selection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Season*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>Summer</td>
<td>Winter</td>
</tr>
<tr>
<td>Forest Openings</td>
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<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Select Harvest/Clear Cut</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Evergreens</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mature Timber</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 2.1. Study area with associated habitat types located within the northern hardwood forested Allegheny Plateau region of Elk County, Pennsylvania.
Figure 2.2. Seasonal 95% home ranges and 50% core areas of Male 1 (3 years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used an oak stand consistently from late summer 2012 to mid-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 2.3. Seasonal 95% home ranges and 50% core areas of Male 5 (3 years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used an oak stand consistently from late summer 2012 to mid-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat. He then started using other oak stands after breeding season in mid-winter during peak snow cover and low food availability.
Figure 2.4. Seasonal 95% home ranges and 50% core areas of Male 47 (5+ years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used oak stands consistently from late summer 2012 to late-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat. He then went to an area in the eastern part of the home range for most of the breeding season. He returned to the oak stands during the third week of November.
CHAPTER 3

BREEDING SEASON MOVEMENTS OF MATURE MALE WHITE-TAILED DEER IN NORTHCENTRAL PENNSYLVANIA

ABSTRACT

Investigation of fine-scale movements of wildlife is critical for understanding the spatial ecology of animals and helping to develop management strategies. Of particular interest to white-tailed deer (*Odocoileus virginianus*) managers and hunters is understanding breeding season behaviors of mature males to enhance management and hunting opportunities. Using GPS technology, we investigated fine-scale (15-minute locations) breeding season movements of 3 mature (≥ 3 years old) male white-tailed deer in a relatively unfragmented northern hardwood forest in the Allegheny Plateau of northcentral Pennsylvania. We used the Dynamic Brownian Bridge Movement Model (DBBMM) to compare movement variances during periods of the breeding season as well as circadian activity patterns. Mature males moved greater distances during the peak rut period resulting in larger weekly home range and core areas. Daytime movements increased up to 8 fold from pre-rut to rut period. We observed notable variations in movements among males, as 1 male moved 4 times as much as another. Weekly home ranges stayed generally within the male’s composite home range, but they focused on different portions of that range during breeding.

INDEX WORDS: breeding season, GPS collars, mature male, movements, rut, white-tailed deer

INTRODUCTION

As deer management continues to place increased focus on enhancing male age structure in many areas (Adams et al. 2009), understanding movements of these animals becomes important for formulating management and population goals. Several studies have reported that
male deer movements increase during peak rut periods, followed by a decrease during the post-rut (Karns 2008, Webb et al. 2010, Foley 2012, Basinger 2013). These increased movements result in home range expansion, which may increase a male’s chance of encountering receptive females (Nelson and Mech 1984, Beier and McCullough 1990, Tomberlin 2007). However, other recent studies indicate that breeding activities are sometimes restricted to previously established home ranges (Hellickson et al. 2008, Webb et al. 2010, Little 2011). In the scrub-shrub habitats of Texas, Foley (2012) even noted a decrease in home range size associated with an increase in mate-search intensity. Webb et al. (2010) found that increased movements during the rut were more linear, indicating that males were actively seeking or pursuing females in estrus.

The movement of mature males in response to hunter pressure appears variable. Karns (2008) and Basinger (2013) observed that movement rates and home range size did not change in response to hunting. Study animals were never pushed outside of their home range and normal behaviors resumed just hours after direct disturbance from a hunter. In contrast, an Oklahoma study indicated that mature males responded to high hunter density (1 hunter/30 ha) by decreasing linear movements and increasing tortuous movements in smaller areas (Little 2011). Males also altered resource selection by seeking security cover, higher elevations, steeper slopes, and areas away from roadways when exposed to human predation risk (Little 2011).

Mate searching behavior described as the dominant floater (Brown 1974), where males covered large portions of their home range with continuous movement, has been confirmed in subsequent studies (Tomberlin 2007, Webb et al. 2010, Basinger 2013). However, mate searching strategies may vary among age classes of males. For example, Foley (2012) described the Levy walk, which consisted of short steps scattered with long step lengths, and Brownian
movements which consisted of constant short step lengths that follow an exponential distribution. In that study, most adult (≥ 3 years old) males demonstrated the Brownian movements, whereas younger (≤ 2 years old) males demonstrated the Levy walk behavior and lower search intensity. Younger males appeared to invest less effort in searching for females, suggesting that they opportunistically pursue females when possible. This suggests that males invest the greatest amount of search effort after physical maturity is reached (Foley 2012).

Prior studies of the breeding season movements of male deer were conducted either in the semi-arid regions of southern Texas, or in fragmented landscapes. Little is known about breeding movements of mature male whitetails in a forested landscape with minimal anthropogenic influence. Therefore, we investigated movements of mature males during the breeding season in a forested landscape in northcentral Pennsylvania.

**STUDY AREA**

We captured mature male deer on an approximately 3,000-ha tract of privately owned land in northcentral Pennsylvania. The entire study area (~6,700 ha) was defined by creating a minimum convex polygon, with a 200-m buffer, around all mature male locations, excluding notable short-interval, long-distance excursions. The study area was centered on the private land where capture activities occurred but also included adjacent state- and privately-owned lands (Figure 1).

Our study site was located within the Allegheny Plateau region of Elk County, PA, and elevations ranged from approximately 430-670 m. The habitat was primarily contiguous forest, consisting mostly of mature or selectively harvested/clearcut northern hardwoods including oaks (*Quercus* spp.), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American basswood (*Tilia americana*), yellow
bitch (*Betula alleghaniensis*), sweet birch (*B. lenta*), eastern hemlock (*Tsuga canadensis*), ash (*Fraxinus* spp.), cucumber magnolia (*Magnolia acuminata*), and tulip poplar (*Liriodendron tulipifera*). Timber harvesting on portions of the study area occurred from the 1990’s to 2005. Residual basal areas ranged from 0 to approximately 50 square feet/acre, which resulted in a dense herbaceous and woody understory across all harvested areas. In contrast, understory vegetation in the areas of mature forest was sparse and consisted primarily of hay-scented fern (*Dennstaedtia punctilobula*), New York fern (*Thelypteris noveboracensis*), and mountain laurel (*Kalmia latifolia*). Small forest openings were also present (1% of the study area), and contained fescue grass (*Festuca* spp.) or agronomic crops planted to supplement native deer forage such as clover (*Trifolium* spp.), forage chicory (*Chicorium intybus*), and brassicas (*Brassica* spp.). Supplemental protein feeding occurred throughout the privately owned land during winter months. Human disturbance on the area consists of only periodic road and food plot maintenance. Hunting pressure is light, consisting of approximately 5 hunter-days /week during the 6 week archery season, and 18 hunter-days /week during the 2-week firearms season. The deer hunting season occurred from 29 September – 8 December 2012.

**METHODS**

**Deer Capture and Handling**

As part of an investigation of seasonal movements of mature male deer, we analyzed the fine-scale breeding season movements of 3 GPS instrumented males. Deer were captured using a combination of free-darting, rocket nets, and clover traps. When free-darting, we used 3-ml transmitter darts (Pneu-dart Inc., Williamsport, PA) to intramuscularly inject a Telazol® (Fort Dodge Animal Health, Fort Dodge, IA)/xylazine hydrochloride (Congaree Veterinary Pharmacy, Cayce, SC) (480mg/315mg) mixture to immobilize deer. We immobilized mature males
captured in rocket nets and clover traps with an intramuscular Telazol®/xylazine hydrochloride (240mg/180mg) injection. To reduce recovery time in cold temperatures we changed immobilization for mature males in rocket nets and clover traps to an injection of 2 ml xylazine hydrochloride (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA). During immobilization, we monitored vital signs, treated for any minor injuries, lubricated eyes, and blindfolded each deer.

While immobilized, each mature male was fitted with a GPS collar (Lotek 3300L; Lotek Wireless Inc., Newmarket, Ontario, Canada or Followit Tellus® 5H1D; Followit AB, Lindesberg, Sweden). Following processing, immobilizing agents were antagonized using 3 ml of Tolazoline HCl (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA). All deer were monitored until fully mobile. Animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (#A2011-08-025-Y1-A0). Deer capture activities were approved by the Pennsylvania Game Commission and conducted under Special Use Permit No. 184-2011.

Data Collection and Monitoring

All mature males were fitted with mortality sensitive GPS collars programmed to collect a position every 15 minutes from 1 October – 31 December 2012. We monitored deer 1 time/week using VHF-telemetry equipment to ensure study animals were alive and that collars were functioning properly.

We used the Lotek GPS 3000 Host Application (Lotek Wireless Inc., Newmarket, Ontario, Canada) and the Followit Tellus TPM Project Manager (Followit AB, Lindesberg, Sweden) software to download positioning data. To decrease the probability of erroneous points in the datasets, non-fix and impossible locations were censored from the dataset. After data
censoring, we imported GPS fixes for each deer into ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) and projected them in Universal Transverse Mercator (UTM) North American Datum (NAD) 1983 Zone 17N (meters). Collar location error (18 meters) was measured by taking mortality events from 4 collars and obtaining the mean X and Y position from 100 random points during the mortality event (stationary collar). The mean position was then plotted in ArcMap and the “point distance” tool in ArcToolbox (Environmental Systems Research Institute, Inc., Redlands, CA) was used to obtain mean distance from GPS locations to mean mortality location.

Data Analysis

We defined the breeding season based on data collected by the Pennsylvania Game Commission, which suggested approximately 80% of females in Pennsylvania were bred from 1 November – 30 November (Pennsylvania Game Commission 2011). Therefore, we defined 3 phases of the rut; pre-rut (1 October – 31 October), rut (1 November – 30 November), and post-rut (1 December – 31 December).

We divided a 24-hour day into dawn, day, dusk, and night. We downloaded sunrise and sunset data for St. Marys, Pennsylvania (12 km from study area) from the United States Naval Observatory website (http:www.usno.navy.mil/USNO) to determine time of day periods. Dawn consisted of the hour before sunrise, the hour that is bisected by sunrise, and the hour after sunrise. Dusk consisted of the hour before sunset, the hour that is bisected by sunset, and the hour after sunset. Day represented the remaining hours between dawn and dusk, while night represented the remaining hours between dusk and dawn (Tomberlin 2007).

We used the Dynamic Brownian Bridge Movement Model (DBBMM) (Kranstauber et al. 2012) package for the R software version 3.0.0 (R Development Core Team 2013) to obtain
movement variances and weekly home ranges of bucks during breeding season. This model constructs utilization distributions based on the movement path of the animal, rather than just the location points, and works well with intensely sampled GPS tracks with failed fixes. A measure of movement behavioral change is created using likelihood statistics to determine change points along an animal’s movement path. It is an improved version of the Brownian Bridge Movement Model (Horne et al. 2007); where it allows the variance of the Brownian motion to fluctuate along the movement path, thus obtaining a more refined movement detection and utilization distribution (Kranstauber et al. 2012). When creating the Dynamic Brownian Bridge Movement Model objects, margin and window size was selected as suggested by Kranstauber et al. (2012) and Byrne et al. (2014).

We used the command “movement pathmetrics” in the software program Geospatial Modelling Environment version 0.7.2.0 (Beyer 2012) to obtain step length distances of movements. This command calculates turn angles, step lengths, bearings, and time intervals for a point time series dataset. We then used the command “rcorr” in program R software version 3.0.0 (R Development Core Team 2013) to see if there was a positive correlation between step length and movement variances. Previous research investigating movement rates of mature males has used step length as a measure of movement (Karns 2008, Tomberlin 2007, Webb et al. 2010, Little 2011, and Basinger 2013). Because step length and Dynamic Brownian Bridge Movement variance had a positive correlation (r = 0.62, P < 0.05), we used the movement variance for analysis because the Dynamic Brownian Bridge method takes into account the step length when measuring movement behavior.
RESULTS AND DISCUSSION

Movement variance (higher value = more movement) was greatest for all males during the peak rut period, but males did not move at the same rate (Figure 3.1) as 1 animal moved 4 times more than the others. Movements during all times of the day increased from pre-rut to rut time period (Figures 3.2). Interestingly, daytime movements even increased 2 to 8 times during this period. We did not see a distinct increase of night time movement compared to other time periods.

Weekly mean home range and core area sizes increased for all males during the peak rut (Figure 3.3). Weekly home ranges during the breeding season stayed generally within the male’s composite home range, but they focused on different portions of that range during breeding. For example, Male 9 focused on different areas of his home range, which changed on a weekly basis (Figure 3.4). Male 5 increased weekly mean home range size during peak rut almost 3 fold, and the core area almost doubled. Male 9 increased weekly mean home range and core area about 1.5 times in size. Male 47 increased weekly mean home range 4 times and core area 3 times in size. This increase of range size along with a major increase in movements during breeding is suggestive of the dominant floater behavior as reported in Tomberlin (2007), Webb et al. (2010), and Basinger (2013).

Increased movement coincident with the rut period likely increases a male’s risk of injury or mortality, and likely his susceptibility to harvest. If a highway exists in a male’s home range, then there may be an increased chance that he would enter the roadway in the potential path of a vehicle. Also with increased movements, the number of encounters with other males would increase, potentially leading to fighting and possible injuries from those battles.
Movements were more evenly distributed among the daily periods and daytime movements were greater than previously reported by Tomberlin (2007). Reduced daytime movement of males in the agricultural landscape investigated by Tomberlin (2007) likely are due to increased human activity on that study area. In contrast, human activity was low and inconsistent on our study area.

Increased movements during the rut resulted in larger weekly mean home range and core area sizes. Increase of breeding season home range size has been observed in previous research and is likely a breeding-related behavior as it increases chances of males encountering receptive females (Nelson and Mech 1984, Beier and McCullough 1990, Tomberlin 2007). Males in our study did not spend significant time outside of composite home ranges, as their breeding activity focused on portions within previously established home ranges. However, area of use within the composite home range changed on a weekly basis. This confinement to established ranges could relate to what Foley (2012) reported concerning focal points of doe activity and spatial memory. Thus, breeding season movements of males within their home range likely is reflective of the spatial distribution of females and activities associated with courting and tending estrous females. It appears that multiple factors such as habitat, landscape scale, and availability of receptive females play a role in mature male breeding season movements.
LITERATURE CITED


Pennsylvania Game Commission. 2011. When is the rut in Pennsylvania?
http://www.portal.state.pa.us/portal/server.pt/community/deer/11949


Figure 3.1. Mean breeding season movement variance created using the Dynamic Brownian Bridge Movement Model ± 95% confidence interval of three mature (≥ 3 years old) males in northcentral Pennsylvania.
Figure 3.2. Mean time of day movement variance created using the Dynamic Brownian Bridge Movement Model ± 95% confidence interval during breeding season of males 5, 9, and 47 in northcentral Pennsylvania. Day time movements increased 8 times (Male 5), 4 times (Male 9), and 2 times (Male 47) from pre-rut to rut.
Figure 3.3. Weekly Dynamic Brownian Bridge home range and core area size (ha) of males 5, 9, and 47 during breeding season in northcentral Pennsylvania.
Figure 3.4. Weekly November Dynamic Brownian Bridge 95% home ranges of Male 9 during breeding season in northcentral Pennsylvania. This animal focused on specific areas that changed weekly within the composite home range, likely pursuing females.
CHAPTER 4

SPRING EXCURSIONS OF MATURE MALE WHITE-TAILED DEER IN
NORTHCENTRAL PENNSYLVANIA

ABSTRACT

During the breeding season, male white-tailed deer have been reported to take excursions outside of their normal home ranges, likely in search of receptive females. During a study in northcentral Pennsylvania, we documented additional excursive movements outside of home ranges that occurred during the spring season. From December 2011 – April 2012 we equipped 13 mature (≥2 years old) male white-tailed deer with GPS collars programmed to record locations hourly. We defined an excursion as any occasion where a male traveled ≥ 1.6 km outside of its 95% home range boundaries for ≥ 12 hours. Between 6 April and 6 June 2012, 9 males (69.2%) made excursions with 6 males making ≥ 2 excursions. Excursions averaged 4.0 km and ranged from 1.7 km to 8.0 km. While the reason for spring excursions is obscure, hypotheses such as increased doe aggression prior to parturition, males returning to natal home ranges, or visitation to mineral sites do not appear tenable based on current observations.

INDEX WORDS: excursions, GPS collars, home range, mature male, movements, spring, white-tailed deer

INTRODUCTION

Understanding how animals navigate their landscape is necessary to understand ecological processes that influence population dynamics, gene flow, and disease transmission. Thus, identification of long- and short-interval excursive behaviors is important. Previous research has reported that both male and female white-tailed deer (*Odocoileus virginianus*) make temporary excursions outside of their normal home range (Tomberlin 2007, Kolodzinski et al. 2010, Karns et al. 2011, Foley 2012, Basinger 2013) during the breeding season. Excursions by
females at this time have been attributed to harassment by rutting bucks, hunting pressure, or active mate selection (Kolodzinski et al. 2010, Basinger 2013). Male excursions likely are related to pursuit of receptive females, but may also occur as males chase off other competing males or isolate receptive females from male competition (Hirth 1977, Tomberlin 2007, Karns et al. 2011, Basinger 2013).

Conventional understanding of deer movement and spatial use indicates that home ranges during late winter and spring often are much smaller than fall ranges, likely due to increased movements during fall associated with breeding activities (Tomberlin 2007, Karns 2008, Webb et al. 2010) as well as seasonal mast availability (McShea and Schwede 1993). As such, the occurrence of fall excursions, as previously reported, is not surprising. However, excursions during other portions of the year have rarely been reported. During a study of the movement ecology of mature male white-tailed deer in northcentral Pennsylvania, we observed that many of our study animals engaged in infrequent, short-term, long-distance movements during the spring. Although Kilgo et al. (1996) reported that some deer (sex not reported) exhibited long-distance, springtime movements in Florida, herein we describe the first reports of spring season excursions by mature male white-tailed deer outside of their normal home ranges.

**STUDY AREA**

We captured deer on an approximately 3,000-ha tract of privately owned land in northcentral Pennsylvania. The entire study area (~6,700 ha) was defined by creating a minimum convex polygon with a 200-m buffer around all deer locations, excluding notable short-interval, long-distance excursions. The study area focused on the private land where capture activities occurred but included state-owned and privately owned adjacent lands. The study site lies on the Allegheny Plateau and elevations ranged from approximately 430-670 m.
The habitat of the study area was primarily contiguous forest, consisting of mostly mature and regenerating northern hardwood forest species including oaks (*Quercus* spp.), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), eastern hemlock (*Tsuga canadensis*), ash (*Fraxinus* spp.), cucumber magnolia (*Magnolia acuminata*), and tulip poplar (*Liriodendron tulipifera*). Small forest openings were also present, and contained fescue grass (*Festuca* spp.) or agronomic crops planted to supplement native deer forage such as clover (*Trifolium* spp.), forage chicory (*Chicorium intybus*), and brassicas (*Brassica* spp.), but encompassed only approximately 1% of the study area. Supplemental protein feeding occurred throughout the privately owned land during the winter months. Human disturbance on the area consists of only periodic road and food plot maintenance. Hunting pressure is light, consisting of approximately 5 hunter-days /week during the 6 week archery season, and 18 hunter-days /week during the 2-week firearms season.

**METHODS**

**Deer Capture and Handling**

We equipped 13 mature (≥ 2.5 years old) male deer with global positioning system (GPS) enabled collars from 15 December 2011 to April 2012. We deployed 3 Lotek 3300L (Lotek Wireless Inc., Newmarket, Ontario, Canada) and 10 Followit Tellus® 5H1D (Followit AB, Lindesberg, Sweden) collars.

We captured deer using a combination of free-darting, rocket nets, and clover traps. When free-darting, we used 3-ml transmitter darts (Pneu-dart Inc., Williamsport, PA) to intramuscularly inject a Telazol® (Fort Dodge Animal Health, Fort Dodge, IA)/xylazine
hydrochloride (Congaree Veterinary Pharmacy, Cayce, SC) (480mg/315mg) mixture to immobilize deer. We immobilized mature males captured in rocket nets and clover traps with an intramuscular Telazol®/xylazine hydrochloride (240mg/180mg) injection. To reduce recovery time in cold temperatures (< -6ºC) we changed immobilization for mature males captured in rocket nets and clover traps to 2 ml xylazine hydrochloride (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA). During immobilization, we monitored vital signs, treated for any minor injuries, lubricated eyes, and blindfolded each deer.

While immobilized, each mature male was equipped with a GPS collar, tightened within 8 cm (approximately 4 fingers width) of the deer’s neck to allow for next swelling associated with the breeding season. We estimated deer age using tooth replacement and wear characteristics (Severinghaus 1949). Live weight was estimated from chest circumference measurements (Pennsylvania Game Commission), and the date and location of each capture was recorded. Each deer also received colored and numbered ear tags (National Band and Tag Co., Newport, KY, USA) to allow for remote visual identification. Following processing, all deer that were injected with Telazol®/xylazine hydrochloride mixture received 3 ml of Tolazoline HCl (100 mg/ml; Lloyd Laboratories, Shenandoah, IA, USA) as an antagonist, administered half intramuscularly and half intravenously, 80 minutes after immobilization injection. Deer immobilized with only xylazine were reversed with 3 ml of Tolazoline HCl, administered half intramuscularly and half intravenously immediately after all data were recorded. All deer were monitored until fully mobile. Animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (#A2011-08-025-Y1-A0). Deer capture activities were approved by the Pennsylvania Game Commission and conducted under Special Use Permit No. 184-2011.
Data Collection and Monitoring

All mature males were fitted with mortality sensitive GPS collars programmed to record hourly fixes throughout deployment. We monitored deer 1 time/week using VHF-telemetry equipment to ensure study animals were alive and that collars were functioning properly. If a mortality or failure signal was detected, the collar was retrieved immediately using radio telemetry. At the end of the study, activation of a remote-release mechanism or a timed release mechanism was used for retrieval of the collars from the field.

Upon collar retrieval, we used the Lotek GPS 3000 Host Application (Lotek Wireless Inc., Newmarket, Ontario, Canada) and the Followit Tellus TPM Project Manager (Followit AB, Lindesberg, Sweden) software to download positioning data. To decrease the probability of erroneous points in the datasets, non-fix and impossible locations were censored from the dataset. After data censoring, we imported GPS fixes for each deer into ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) and projected them in Universal Transverse Mercator (UTM) North American Datum (NAD) 1983 Zone 17N (meters). Collar location error (18 meters) was measured by taking mortality events from 4 collars distributed throughout the study area and obtaining the mean X and Y position from 100 random points during the mortality event (stationary collar). The mean position was then plotted in ArcMap and the “point distance” tool in ArcToolbox (Environmental Systems Research Institute, Inc., Redlands, CA) was used to obtain mean distance from GPS locations to mean mortality location.

Data Analysis

We used the hourly fixes to construct seasonal home ranges and core areas. We constructed 95% home ranges and 50% core areas using the Dynamic Brownian Bridge Movement Model (hereafter, DBBMM; Kranstauber et al. 2012) Package for the R software
version 3.0.0 (R Development Core Team 2013). Briefly, this model converts point locations to movement paths and uses them to construct utilization distributions. The DBBMM works well with intensively-sampled GPS tracks that include failed or missing fixes. The model uses likelihood statistics to determine change points along an animal’s movement path, and creates a measure of movement-based behavioral changes. In contrast to the original Brownian Bridge Movement Model (Horne et al. 2007), the DBBMM allows the variance of Brownian motion to fluctuate along the movement path, creating a more refined utilization distribution (Kranstauber et al. 2012). We selected model objects, margin and window size as suggested by Kranstauber et al. (2012) and Byrne et al. (2014). We defined the spring season based from the astronomical calendar but still remaining biologically meaningful, as 20 March – 20 June when snow cover starts to deplete followed by green up. We used the command movement pathmetrics in the software program Geospatial Modelling Environment version 0.7.2.0 (Beyer 2012) to obtain step length distances of excursions. This command calculates turn angles, step lengths, bearings, and time intervals for a point time series dataset. Excursions were defined as any occasion where a buck traveled ≥ 1.6 km outside of its 95% home range boundaries for ≥ 12 hours.

RESULTS AND DISCUSSION

Nine of 13 (69.2%) males demonstrated spring season excursions from 6 April through 6 June, with 6 males making multiple excursions (Table 4.1). Mean excursion distance from the home range boundary was 4.0 km (range = 1.7 – 8.0 km). Mean direction of the excursions was 192 degrees (Figure 4.1). Mean duration of excursions was 22 hrs (range = 12 – 40 hrs), and step length averaged 11.0 km (range = 5.2 – 21.8 km). One male (#1) engaged in 7 separate excursions with the greatest path distance traveled being 16.4 km in 30 hrs (Figure 4.2). This animal was accompanied by another male (#5) on 5 of these excursions, the longest of which
covered 12.6 km total path distance and lasted 30 hrs (Figure 4.3). As a result of the close association between animals #1 and #5, their spring home ranges and core areas were similar. Male #7 made 1 excursion for 12 hrs with a total path distance of 5.5 km (Figure 4.4) whereas Male #9 made 2 excursions with the longest path distance traveled being 11.6 km in 16 hrs (Figure 4.5). Male #17 made 2 excursions, with the longest path distance of 16.8 km for 19 hrs (Figure 4.6). Male #18 made 1 excursion for 38 hrs and traveled a path distance of 12.6 km (Figure 4.7). Male #24 made 2 excursions with the longest time being 36 hrs, and the longest distance traveled 12.3 km (Figure 4.8). Male #28 made 5 excursions, with the longest path distance being 21.8 km for 40 hrs (Figure 4.9). This animal accompanied Male #24 on both of his excursions, and both males had similar spring home ranges and core areas. Male #38 made 1 excursion for 15 hrs, with a total path distance of 11.3 km (Figure 4.10). Four GPS-equipped mature males did not make any excursive movements during spring. The excursions observed were similar in duration, distance, and direction of travel for all bucks. These excursions lasted no longer than 40 hrs and the primary direction of travel was to the south, much different than the excursions Kilgo (1996) reported in Florida.

Although Kilgo et al. (1996) provided evidence of springtime excursions by white-tailed deer in Florida, the frequency of spring excursions and the age and sex characteristics of deer engaging in these excursions was not reported. To our knowledge, we are the first to identify and describe the occurrence, timing, and directionality of spring excursions of mature male white-tailed deer. All excursions occurred between 6 April and 6 June, with a mean date of 2 May, we observed no temporal patterns of dispersals among individuals that would suggest a seasonal or climatic cue (Figure 4.11). Of the 26 excursions, more than 50% were made within a
1-month period prior to parturition ($\bar{X} = 6$ June, ranging from 26 April- 5 September) (Pennsylvania Game Commission 2011).

Female aggression associated with pre-parturition and neonatal territoriality (Hirth 1977, Ozoga et al. 1982, Schwede et al. 1993, Bertrand et al. 1996, and D’Angelo et al. 2004) might lead bucks to temporarily leave an area. However, we observed that all males invariably returned to their typical range within a short time period (<40 hrs). In addition, many excursions occurred months prior to parturition, suggesting a maternal aggression cue is unlikely. Further, no excursions were observed after 5 June, and if maternal aggression was a causative factor, one would expect excursions to last throughout the fawn-rearing seasons.

Kilgo et al. (1996) hypothesized that spring and fall excursions by adult deer may represent return trips to natal ranges. However, in the Allegheny Plateau of Pennsylvania, average dispersal distance is 8.0 +/- 0.61 km with a maximum dispersal distance of 40.6 km (Long et al. 2008). In contrast, the excursions by mature males that we observed averaged 4.0 +/- 0.36 km and ranged from 1.7 km to 8.0 km, much shorter than reported dispersal distances. Further, 23 of 26 excursions (88.5%) were made in the south or southwest direction, while only 2 excursions were to the northwest, and one was to the east. In Pennsylvania and Florida, dispersal movements from natal ranges tended to follow an east or east-west axis (Kilgo et al. 1996, Newberry et al. 2004). Thus, with the comparatively short distances and southerly orientation of most spring excursions, it appears unlikely that a return to their natal range is a proximate factor.

A final hypothesis for spring excursions is that males are visiting mineral sites. To the south of the property is a paved township road where anti-slip containing salt is used during the winter months. Salt deposits would be present alongside the road during the spring after snow melt. In West Virginia, Campbell et al. (2004) reported that 30 of 121 (25%) of radio collared
deer traveled a mean distance of 3.0 km (0.9 – 5.5 km) to a gas well site to consume water from a ground seep, which tested for high concentrations of sodium. Sodium deficiencies during the spring and summer months often cause deer to seek sodium sources (Weeks and Kirkpatrick 1976), which may occur outside their normal home range (Wiles and Weeks 1986). However, analysis of excursion destinations, where males spent several hours, did not show any mineral attractant. Furthermore, manmade mineral sites are abundant throughout the study site and at least 1 mineral site was present in the spring home ranges of all males. Thus it is unlikely that mineral lick visitation was a factor influencing the occurrence of excursions.

Similar to dispersal movements, spring and fall excursions in Florida were highly directional, with most excursions occurring along an east-west axis (Kilgo et al 1996). In Florida, no landscape features that could influence directionality of movements were apparent. Similarly, our observations of excursions in this study suggest that movement were highly linear and independent of topographic features.

While spring excursions may be a common occurrence in white-tailed deer populations, they have not been commonly reported in previous studies, perhaps due to the dearth of studies employing GPS technology during this time of year. Alternatively, in the highly fragmented habitats typical of the whitetail’s range, excursive behaviors would be risky as deer are exposed to unfamiliar open areas and highways. Future investigations should seek to examine if these excursions occur across white-tailed deer populations, and the spatial associations these males make with the landscape as they traverse unfamiliar territories.
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Table 4.1. Excursions of mature (≥ 3 years old) male white-tailed deer during the spring season in northcentral Pennsylvania during 2012. Excursions were defined as traveling ≥ 1.6 km outside of its 95% home range boundaries for ≥ 12 hours. Home ranges were created using the Dynamic Brownian Bridge Movement Model.

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Mean 5/2 00:04 5/2 22:57 22 ± 1.70 192 ± 8.3 4.0 ± 0.36 11.0 ± 0.85
Figure 4.1. Direction and distance (km, measured from perimeter of spring 95% DBBMM home range) of 26 excursions made by 9 mature (≥ 3 years old) male white-tailed deer during the spring season in northcentral Pennsylvania. Mean direction was 192° with a standard error of 8.3.
Figure 4.2. One of the 7 spring excursions (longest) made by Male #1 (3 years old) in northcentral Pennsylvania. On 6 April 2012 this animal traveled a total path distance of 16.4 km in 30 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4.3. One of the 5 spring excursions (longest) made by Male #5 (3 years old) in northcentral Pennsylvania. On 6 April 2012 this animal traveled a total path distance of 12.6 km in 30 hours (accompanied by Male #1) outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4.4. Spring excursion made by Male #7 (4 years old) in northcentral Pennsylvania. On 13 May 2012 this animal traveled a total path distance of 5.5 km in 12 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4.5. Spring excursions of Male #9 (4 years old) in northcentral Pennsylvania. On 2 June 2012 and 28 April 2012 this animal traveled a path distance of (A) 11.6 km in 16 hours and (B) 5.2 km in 13 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 4.6. Spring excursions of Male #17 (4 years old) in northcentral Pennsylvania. On 5 May 2012 and 18 April 2012 this animal traveled a path distance of (A) 16.8 km in 19 hours and (B) 8.7 km in 18 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 4.7. Spring excursion made by Male #18 (4 years old) in northcentral Pennsylvania. On 6 April 2012 this animal traveled a total path distance of 12.6 km in 38 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4.8. Spring excursions of Male #24 (3 years old) in northcentral Pennsylvania. On 28 April 2012 and 12 April 2012 this animal traveled a path distance of (A) 12.3 km in 27 hours and (B) 8.4 km in 36 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 4.9. One of the 5 spring excursions (longest) made by Male #28 (3 years old) in northcentral Pennsylvania. On 11 May 2012 this animal traveled a total path distance of 21.8 km in 40 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
**Figure 4.10.** Spring excursion made by Male #38 (5+ years old) in northcentral Pennsylvania. On 29 April 2012 this animal traveled a total path distance of 11.3 km in 15 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4.11. Date of occurrence and distance (km) from edge of 95% home range of mature (≥3 years old) male white-tailed deer excursions in northcentral Pennsylvania, Spring 2012.
CHAPTER 5
SUMMARY AND CONCLUSIONS

With the increasing numbers of mature males in white-tailed deer populations across the United States, it is important to understand their use of landscapes and how to properly manage habitats, harvest rates, and potentially the spread of disease. My results are indicative of the importance of both scale and diversity in managing deer in Northeastern climates with the goal of increasing representation of mature males in the herd. In a northern hardwood forested landscape, disturbance through either timber harvest or creation of forest openings creates habitats readily selected by males when establishing and maintaining home ranges and core areas. Therefore, managers should recognize the importance of maintaining forest communities with diverse successional stages to provide males with necessary resources.

My results indicated mature males moved greater distances during the peak rut period resulting in larger weekly home range and core areas. Daytime movements increased up to 8 times from pre-rut to rut period. Movement patterns varied among males with as much as a 4-fold difference in movement among individuals. Males in my study did not spend significant time outside of composite home ranges, as their breeding activity focused on portions within previously established home ranges. However, area of use within the composite home range changed on a weekly basis.

To my knowledge, I am the first to identify and describe the occurrence, timing, and directionality of spring excursions of mature male white-tailed deer. While the reason for spring
excursions is obscure, hypotheses such as increased doe aggression prior to parturition, males returning to natal home ranges, or visitation to mineral sites do not appear tenable based on current observations. Future investigations should seek to examine if these excursions occur across white-tailed deer populations, and the spatial associations these males make with the landscape as they traverse unfamiliar territories.
APPENDIX A

SEASONAL HOME RANGES AND CORE AREAS OF ADULT MALE WHITE-TAILED DEER WITH ASSOCIATED HABITATS IN NORTHERN PENNSYLVANIA
Figure 1. Seasonal 95% home ranges and 50% core areas of Male 1 (3 years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used an oak stand consistently from late summer 2012 to mid-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 2. Seasonal 95% home ranges and 50% core areas of Male 2 (3 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 3. Seasonal 95% home ranges and 50% core areas of Male 5 (3 years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used an oak stand consistently from late summer 2012 to mid-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat. He then started using other oak stands after breeding season in mid-winter during peak snow cover and low food availability.
Figure 4. Seasonal 95% home ranges and 50% core areas of Male 7 (4 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 5. Seasonal 95% home ranges and 50% core areas of Male 9 (4 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 6. Seasonal 95% home ranges and 50% core areas of Male 10 (5+ years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 7. Seasonal 95% home ranges and 50% core areas of Male 17 (4 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 8. Seasonal 95% home ranges and 50% core areas of Male 18 (4 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
**Figure 9.** Seasonal 95% home ranges and 50% core areas of Male 19 (4 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 10. Seasonal 95% home ranges and 50% core areas of Male 24 (3 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 11. Seasonal 95% home ranges and 50% core areas of Male 28 (3 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 12. Seasonal 95% home ranges and 50% core areas of Male 38 (5+ years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 13. Seasonal 95% home ranges and 50% core areas of Male 45 (5 years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 14. Summer 95% home range and 50% core area of Male 46 (5+ years old) in northcentral Pennsylvania in a northern hardwoods habitat.
Figure 15. Seasonal 95% home ranges and 50% core areas of Male 47 (5+ years old) during 2012-2013 based on Dynamic Brownian Bridge Movement Model. This animal used oak stands consistently from late summer 2012 to late-October 2012 in northcentral Pennsylvania in a northern hardwoods habitat. He then went to an area in the eastern part of the home range for most of the breeding season. He returned to the oak stands during the third week of November.
APPENDIX B

SPRING SEASON EXCURSIONS OF ADULT MALE WHITE-TAILED DEER IN NORTHERN PENNSYLVANIA
Figure 1. One of the 7 spring excursions (longest) made by Male #1 (3 years old) in northcentral Pennsylvania. On 6 April 2012 this animal traveled a total path distance of 16.4 km in 30 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 2. Second of the 7 spring excursions made by Male #1 (3 years old) in northcentral Pennsylvania. On 18 April 2012 this animal traveled a total path distance of 10.1 km in 29 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 3. Third of the 7 spring excursions made by Male #1 (3 years old) in northcentral Pennsylvania. On 30 April 2012 this animal traveled a total path distance of 9.3 km in 15 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 4. Fourth of the 7 spring excursions made by Male #1 (3 years old) in northcentral Pennsylvania. On 5 May 2012 this animal traveled a total path distance of 6.1 km in 14 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 5. Fifth of the 7 spring excursions made by Male #1 (3 years old) in northcentral Pennsylvania. On 16 May 2012 this animal traveled a total path distance of 6.3 km in 14 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 6. Sixth of the 7 spring excursions made by Male #1 (3 years old) in northcentral Pennsylvania. On 18 May 18, 2012 this animal traveled a total path distance of 7.9 km in 14 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 7. Final spring excursion made by Male #1 (3 years old) in northcentral Pennsylvania. On 26 May 2012 this animal traveled a total path distance of 10.2 km in 27 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 8. One of the 5 spring excursions (longest) made by Male #5 (3 years old) in northcentral Pennsylvania. On 6 April 2012 this animal travele[d a total path distance of 12.6 km in 30 hours with Male #1 outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 9. Second of the 5 spring excursions made by Male #5 (3 years old) in northcentral Pennsylvania. On 18 April 2012 this animal traveled a total path distance of 10.0 km in 29 hours with Male #1 outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 10. Third of the 5 spring excursions made by Male #5 (3 years old) in northcentral Pennsylvania. On 30 April 2012 this animal traveled a total path distance of 9.4 km in 15 hours with Male #1 outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 11. Fourth of the 5 spring excursions made by Male #5 (3 years old) in northcentral Pennsylvania. On 16 May 2012 this animal traveled a total path distance of 6.4 km in 14 hours with Male #1 outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 12. Final spring excursion made by Male #5 (3 years old) in northcentral Pennsylvania. On 26 May 2012 this animal traveled a total path distance of 10.3 km in 27 hours with Male #1 outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 13. Spring excursion made by Male #7 (4 years old) in northcentral Pennsylvania. On 13 May 2012 this animal traveled a total path distance of 5.5 km in 12 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 14. Spring excursions of Male #9 (4 years old) in northcentral Pennsylvania. On June 2012 and 28 April 2012 this animal traveled a path distance of (A) 11.6 km in 16 hours and (B) 5.2 km in 13 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 15. Spring excursions of Male #17 (4 years old) in northcentral Pennsylvania. On 5 May 2012 and 18 April 2012 this animal traveled a path distance of (A) 16.8 km in 19 hours and (B) 8.7 km in 18 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 16. Spring excursion made by Male #18 (4 years old) in northcentral Pennsylvania. On 6 April 2012 this animal traveled a total path distance of 12.6 km in 38 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 17. Spring excursions of Male #24 (3 years old) in northcentral Pennsylvania. On 28 April 2012 and 12 April 2012 this animal traveled a path distance of (A) 12.3 km in 27 hours and (B) 8.4 km in 36 hours outside of its 95% spring home range created using the Dynamic Brownian Bridge Movement Model.
Figure 18. First of the 5 spring excursions made by Male #28 (3 years old) in northcentral Pennsylvania. On 12 April 2012 this animal traveled a total path distance of 9.3 km in 12 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 19. Second of the 5 spring excursions made by Male #28 (3 years old) in northcentral Pennsylvania. On 17 April 2012 this animal traveled a total path distance of 6.5 km in 25 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 20. Third of the 5 spring excursions made by Male #28 (3 years old) in northcentral Pennsylvania. On 28 April 2012 this animal traveled a total path distance of 14.1 km in 25 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 21. Fourth of the 5 spring excursions (longest) made by Male #28 (3 years old) in northcentral Pennsylvania. On 11 May 11, 2012 this animal traveled a total path distance of 21.8 km in 40 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 21. Final spring excursion made by Male #28 (3 years old) in northcentral Pennsylvania. On 5 June 2012 this animal traveled a total path distance of 20.3 km in 28 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).
Figure 23. Spring excursion made by Male #38 (5+ years old) in northcentral Pennsylvania. On 29 April 2012 this animal traveled a total path distance of 11.3 km in 15 hours outside of its 95% spring home range (Dynamic Brownian Bridge Movement Model).