Movement of Female White-tailed Deer Relative to Conception and Localized Risk

by

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Abstract

There are few data available that describe the spatial patterns of female white-tailed deer relative to their date of conception. To address this paucity of information, I placed GPS collars on free ranging female white-tailed deer, and combined the spatio-temporal data collected with information regarding each deer's conception. My results indicate that female white-tailed deer engage in excursive behavior surrounding conception, likely as a means to maximize the number of potential mates aware of breeding receptivity.

Similarly, little is known concerning the ability of white-tailed deer to detect and respond to localized risks, such as those posed by human hunters. By pairing GPS collar data with information about the usage of specific hunting locations I was able to examine how deer respond to risk at individual locations. My results indicate that deer perceive localized instances of risk and respond accordingly, but such responses may not be apparent without accounting for the localized nature of risk.

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Abstract

Female white-tailed deer (*Odocoileus virginianus*) are believed to perform two behavioral strategies to maximize the quality of potential mates: sit and wait, characterized by concentrating activity within a core area, and excursive behavior, characterized by increased activity and excursions outside the home range. However, there are few data available that describe the spatial patterns of female white-tailed deer relative to their date of conception, and thus it is unknown whether one or both of these behavioral strategies utilized. Our goal was to examine spatial patterns of female white-tailed deer to determine the breeding strategies that are employed. We equipped 36 female white-tailed deer with GPS collars from August-December 2013-2015. Movement rate, probability of activity, probability of being outside the home range, home range size, core area size, and core area:home range ratio were calculated for each deer relative to three breeding stages and individual date of conception. Additionally, the paths of deer which conceived were examined for excursions. Movement rate and probability of activity both peaked near the peak of the breeding season and rapid increases were observed during the 40 days prior to conception for both metrics. Home range and core area size were greatest later in the breeding season, with peak values occurring in the days surrounding conception. Eleven deer performed an excursion, ranging from 43 days before until 36 days following conception, with the peak probability of being outside of the home range occurring 1 day prior to conception. Our data suggest that female white-tailed deer maximize the quality of their mates by advertising

their availability for breeding through excursive behaviors and other spatial patterns just prior to entering estrus.

Introduction

An animal’s fitness, or the extent to which it contributes genetic material to subsequent generations, is inherently determined by reproductive success and the success of progeny (Freeman and Herron 2004). However, due to the inequity in parental investment found in the majority of polygynous species (Trivers 1972; Smith 1977; Raven and Johnson 2001), advantageous methods to increase fitness vary between the sexes. Male reproductive output is limited only by the number of females successfully bred, and as sperm is relatively inexpensive to produce, males can increase fitness by minimizing selectivity and breeding as many females as possible (Raven and Johnson 2001). Meanwhile, females face significantly greater investment due to the demands of gestation and lactation (Clutton-Brock et al. 1989; Speakman 2008), along with possible tradeoffs between current and future reproduction (Stearns 1992; Del Giudice et al. 2015). Therefore, a female can best improve fitness by maximizing mate quality, which is generally achieved through a high degree of selectivity (Raven and Johnson 2001). By breeding with a high quality male, females provide offspring with advantages in areas such as future reproductive potential and immunocompetence (von Schantz et al. 1994; Ditchkoff et al. 2001). However, as females near the end of receptivity, fitness benefits accrued from breeding with a high quality male may be outweighed by the benefits of conceiving during the first estrus (predator swamping, and increased growth of offspring before their first winter; Zwank and Zeno 1986; Whittaker and Lindzey 1999; Gray et al. 2002), causing her to breed with a lower quality male rather than risk not reproducing in the first estrous cycle.

Due to the fitness benefits of breeding with a high quality male, behavior of females approaching receptivity is likely a function of herd demographics. An example of this is found in white-tailed deer (*Odocoileus virginianus*), where previous studies have documented two behavioral strategies employed by does during the breeding season. The first strategy, known as "sit and wait", has been observed near the peak of the breeding season and is characterized by a decrease in movement rate and home range size, and an increase in core area use (Ivey and Causey 1981; Holzenbein and Schwede 1989; Beir and McCullogh 1990). Sit and wait behavior theoretically allows a female to be easily located by roaming bucks, as she is in a predictable location well marked with scent indicators expressing receptivity (Holzenbein and Schwede 1989; Beir and McCullogh 1990; Labisky and Fritzen 1998). Since the sit and wait strategy forces a doe to utilize a small area this approach relies on females being a limiting resource, and assumes that bucks will exhibit intensive search behaviors. Therefore, the sit and wait strategy is theorized to be most likely to occur in populations with high deer densities and high buck:doe ratios (Holzenbein and Schwede 1989; Beir and McCullogh 1990; Labisky and Fritzen 1998). The sit and wait strategy is advantageous for the female as it allows her to reduce energy expenditure and limit her risk of mortality by remaining in a familiar area (Labisky and Fritzen 1998).

A second behavioral strategy observed in female white-tailed deer during the breeding season is excursive behavior. Excursive behavior is generally characterized by increased activity leading to an excursion outside of the home range (Sawyer 1981; D'Angelo et al. 2004; Kolodzinski et al. 2010). Previous work has described these excursions as brief, lasting an average of 24-hours, and variable in distance, ranging from 0.57 - 4.78 km (Kolodzinski et al. 2010). It has been hypothesized that excursive behavior improves a female's opportunity of encountering a mate during her short period of receptivity (Ozoga and Verme 1975), particularly in populations that are characterized by low deer density or a female-biased sex ratio (Holzenbein and Schwede 1989; Beir and McCullogh 1990; Labisky and Fritzen 1998; D’Angelo et al. 2004; Kolodzinski et al. 2010). Excursive behavior has also been documented in other cervids such as roe deer (*Capreolus capreolus*; Lovari et al. 2008; Richard et al. 2008; Debeffe et al. 2014) and red deer (*Cervus elaphus*; Stopher et al. 2011). The predominant belief is that excursive behavior may be an effort to maximize the probability of finding a male during the short period that the doe is receptive (Holzenbein and Schwede 1989; Labisky and Fritzen 1998; D’Angelo et al. 2004). However, since excursions have been documented in populations with both high (Ivey and Causey 1981; Kolodzinski et al. 2010) and low deer densities (D’Angelo 1994; Labisky and Fritzen 1998), some have conjectured that excursive behaviors during the breeding season may be a form of direct female mate choice (Kolodzinski et al. 2010; Hasapes 2012), or a means to incite male competition and access a higher quality mate (Cox and Le Boeuf 1977).

Unfortunately, there is a major gap in our understanding of deer breeding behavior. Each study that has previously documented the breeding season movement patterns of free ranging female white-tailed deer has done so only at the broad scale of population breeding stages (ie. prerut, rut, postrut; Sawyer 1981; Holzenbein and Schwede 1989; Beir and McCullogh 1990; Labisky and Fritzen 1998; D’Angelo et al. 2004; Kolodzinski et al. 2010). While previous studies have identified general behavioral patterns of females during the breeding season, they have failed to improve our understanding of the behavioral and spatial tendencies of females relative to their specific conception date and do not allow for inference as to any breeding or mate selection strategies that are employed by females. Therefore, evaluating the movement of female white-tailed deer relative to conception is a clear next step in understanding not only how female large mammals utilize space during a key life history event, but also in exploring the possibility of female mate choice. The goal of this project was to examine the movement and space use patterns of female white-tailed deer during periods relevant to breeding at the population and individual levels. Our specific objectives were to: (1) characterize activity patterns of free ranging female white-tailed deer relative to the populations' peak of conception, (2) characterize activity patterns relative to individual conception, and (3) determine if the observed behaviors are breeding related.

Methods

Study Area

Our research was conducted at Brosnan Forest, a 5,830-ha tract of lower coastal plain habitat in Dorchester County, South Carolina (N 33'08.951, W 80'25.726). This project took place exclusively on the 2,552-ha portion of the property located north of Highway 78. Deer density on this property had been estimated at 20/km^2 with a buck to doe ratio of 1:1.4 (J.B. Raglin, Norfolk Southern Railway, unpublished data). McCoy et al. (2013) reported a peak of conception on 9 October for Brosnan Forest, with 80% of conceptions occurring between 19 September and 28 October. Approximately 93% forested, the study area contained mostly open longleaf pine (*Pinus palustris*) stands interspersed with mixed hardwoods (Collier et al. 2007). Hardwood drains were found throughout the property with mixed pine-hardwood areas comprised of loblolly (*Pinus taeda*), slash (*Pinus elliottii*), and pond (*Pinus serotina*) pine, along with oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Bottomland drains included oak, sweetgum, black gum (*Nyssa sylvatica*), and yellow poplar (*Liriodendron tulipifera*). The majority of forest stands were actively managed for wildlife and timber production and were burned on a 2-3 year rotation to maintain an open understory (Lauerman 2007; Collier et al. 2007). Food plots on the study area ranged in size from 0.03-8.5 hectares, and comprised a total of 119 hectares. While a majority of plots were planted annually with a cool season mix of various clovers (*Trifolium* spp.), grains (oats, *Avena fatua*; wheat, *Triticum aestivum*), chicory (*Cichorium intybus*), and winter peas (*Pisum sativum*), additional plots received spring plantings of soybeans (*Glycine max*), sorghum (*Sorghum bicolor*), or game bird mix containing sorghum (*Sorghum bicolor*), buckwheat (*Fagopyrum esculentum*), benne (*Sesamum indicum*), and sunflower (*Helianthus* spp.). There were also 54-55 feeders, depending on year, distributed throughout the study area dispensing shelled corn during the hunting season which, though it ran from 15 August-1 January in this portion of South Carolina, did not begin until 15 September on Brosnan Forest.

Capture

During May-August of 2013-2015, a total of 43 female white-tailed deer (≥1 year old) were immobilized via a 2cc transmitter dart (Pneu-dart Inc., Williamsport, Pennsylvania, USA) containing a Xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 2.2 mg/kg) and Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 100mg/ml given at a rate of 4.5 mg/kg) mixture. Deer were fitted with an ATS G2110D GPS Collar (Advanced Telemetry Systems, Isanti, Minnesota) tightened to within approximately two finger widths of the neck, allowing the collar to stay in the proper upright position thereby improving data accuracy (D'Eon and Delaparte 2005). After processing was complete a 3-ml intramuscular injection of Tolazoline (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 6.6 mg/kg) was administered to act as a reversal to the Xylazine/Telazol mixture, and deer were observed until they moved away under their own power. All protocols involving animals were approved by the Auburn University Animal Care and Use Committee (PRN# 2013-2205).

Data Collection and Manipulation

GPS collars were programmed to take fixes at 30-minute intervals from 16 August-1 December, recording position in UTM coordinates, date, time, altitude, fix status, satellites, position dilution of precision (PDOP), horizontal dilution of precision (HDOP), and temperature. Data were offloaded using ATS WinCollar software, and likely erroneous 3-dimensional fixes with PDOP > 10 or HDOP > 6, and 2-dimensional fixes with HDOP > 3 were removed (D'Eon and Delparte 2005; Lewis et al. 2007). Collared deer were eligible for hunter harvest beginning in December and harvested animals were taken to a central processing facility where harvest location and time, age, weight, and pregnancy status were recorded. All deer were aged via tooth wear and replacement (Severinghaus 1949). All fetuses were removed from pregnant animals, and date of conception was back calculated using a fetal aging scale (Hamilton et al. 1985).

All spatial data were classified using two separate approaches. First, following the classification system of previous studies (Sawyer 1981; Holzenbein and Schwede 1989; Beir and McCullogh 1990; Labisky and Fritzen 1998; D'Angelo et al. 2004; Kolodzinski et al. 2010), each fix was assigned as being either prerut, rut, or postrut. In our study, those periods ranged from 16 August – 18 September, 19 September- 28 October, and 29 October –1 December, respectively. These dates were determined such that the rut period would account for 80% of all conceptions previously documented on the study site (McCoy et al. 2013). Secondly, for all deer that conceived during the study, each fix ranging from 45 days prior to conception to 45 days post conception was assigned a value describing the number of days from conception that the fix took place. This range was utilized because it was sure to encompass movements both leading up to and after conception, as it was greater than the 28-day estrous cycle of female white-tailed deer (Plotka et al. 1977). Examining activity at both population breeding stages and relative to date of conception allowed us to compare movements of individuals to population level trends from this study and previously reported studies, and thereby determine if behaviors observed in this population are site specific or potentially representative of white-tailed deer in general.

We identified 6 spatial metrics (movement rate, home range size, core area size, core area:home range ratio, probability of being outside the seasonal home range, and the probability of activity) that we hypothesized could be impacted by breeding-related activity. Movement rate was calculated by finding the average Euclidean distance between consecutive half hour fixes throughout a single day (Root et al. 1988; Labisky and Fritzen 1998; Webb et al. 2010). Similar to the censoring method applied by Webb et al. (2010), only days with at least half of the possible consecutive fixes were utilized. Movement rate was utilized because it quantifies movement during a given period, providing insight into the degree of activity displayed by the animal. Movement rate, or a similar representation of movement, has been widely used in the deer literature and allows for comparisons of results between studies (Holzenbein and Schwede 1989; Labisky and Fritzen 1998; D'Angelo et al. 2004; Kolodzinski et al. 2010; Webb et al. 2010). We calculated home range and core use areas for each deer using the Brownian bridge method (Horne et al. 2007) for the entire study period (seasonal home range), as well as for the prerut, rut, and postrut periods. The 95% and 50% isopleths were used for the home range and core area estimates, respectively. Additionally, for deer that conceived, home ranges and core area sizes were calculated for 13, 7-day periods from 45 days before until 45 days after conception. The area of each home range and core area was calculated using ArcMap 10.2 (ArcMap version 10.2, ESRI Inc., Redlands CA, 2013). Home range and core area sizes describe the spatial extent of animal movements and are widely utilized in studies examining animal behavior (Kie et al. 2010). Core area:home range ratio was calculated by dividing core area size by home range size. This ratio allows for characterization of the intensity of an individual's use of space, where a ratio close to 1 indicates an individual is using its entire home range equally and a ratio close to 0 suggests that an individual is using small portions of its home range much more intensively (Rotem et al. 2011; Monsarrat et al. 2013). To find the probability of being outside the seasonal home range (SHR) each fix was recorded as within or not within the SHR. The probability of a deer being outside the SHR provides information about an individual's propensity to travel outside of its home range and engage in exploratory movements (Kolodzinski et al. 2010).Probability of activity was calculated daily for each 30-minute interval within 3 separate periods: the 24-hr day, diurnal hours, and nocturnal hours. Diurnal hours ranged from one half hour before sunrise until one half hour after sunset, with nocturnal being the remainder of the 24-hr day. Probability of activity was treated as a binary variable, and an individual was considered to be active in a 30-minute interval if the distance between consecutive locations was greater than the predetermined threshold distance of 51.78 m according to Sullivan et al. (2016).

Finally, movement paths of all individuals found to have conceived were manually inspected for excursions outside of the seasonal home range. Similar to previous studies (Kolodzinski et al. 2010; Karns et al. 2011), an excursion was defined as (1) any series of fixes outside of the seasonal home range which extended $\geq$ 0.5 km, or (2) when half of an animal's daily fixes were outside of the seasonal home range. When an excursion was identified, the date and days from conception were recorded.

Data Analysis

Movement rate, home range and core area size, and home range to core area ratio were analyzed relative to population breeding stages using general linear models (metric ~ rut stage), while likelihoods of activity and being outside the SHR were analyzed via generalized linear models. Probabilities were estimated from the statistical model. General linear models were used to analyze home range size, core area size, and core area:home range ratio relative to date of conception, with movement rate, probability of activity, and probability of being outside the SHR analyzed via generalized additive modelling (metric ~ days to conception). Finally, the probability of an excursion occurring each day from conception was calculated via a general linear model with a second degree polynomial. Logistic regression was used to determine if the likelihood of a deer performing an excursion was impacted by the age of the deer. All analyses were conducted in R (v3.1.3; R Core Development Team 2015).

Results

During the study, 2 deer died prior to the beginning of the study period, 2 collars malfunctioned, and 3 collars were not recovered at the time of data analysis, leaving a total of 36 deer. These 36 collars had an average fix success rate, after data censoring, of 87.61% (n = 163,508) while the stationary collars had an average fix success rate of 99.87% (n = 792). Thirty-two collared deer with an average age of 3.8 years (SE = 0.2) were hunter harvested following the study period, and conception was documented in 21 of these animals. Conceptions ranged from 11 September-2 November, with 80.95% occurring during the rut period.

There was a general trend of increasing activity from the prerut to the rut when examining movement rate, probability of activity, probability of being outside the SHR, home range size, core area size, and core area:home range (Table 1.1). Movement rate, probability of activity, and probability of being outside the SHR all increased from prerut to rut, and while movement rate and probability of activity declined from rut to postrut, probability of being outside the SHR continued to rise during this period. The space use metrics of core area and home range size both increased from prerut to rut, while core area:home range did not. However, while home range size continued to increase from rut to postrut, core area size and core area:home range values declined. When examined relative to date of conception, there was a tendency for activity metrics (movement rate and probability of activity) to steadily increase during the 40 days prior to conception, level off or slightly decrease in the days around conception, and then increase once again until 15-20 days following conception (Figure 1.1; Figure 1.2). Probability of activity during both diurnal and nocturnal hours closely resembled Probability of activity during the 24-hour day, though it was consistently greater at night. Home range and core area were both greatest during the weeks surrounding conception, with values of 17.284 ha (SE = 0.826), and 2.966 ha (SE = 0.165), respectively (Figure 1.3). However, core area:home range surrounding conception was not different from any other period.

Of the 21 deer that conceived, 11 went on at least 1 excursion, with a total of 23 recorded excursions. There were 2, 14, and 7 excursions performed during the prerut, rut, and postrut periods, respectively, and excursions ranged from 43 days prior to 36 days post conception (Table 1.2). The probability of a deer going on an excursion on a particular day increased rapidly prior to conception, and peaked at 0.045 (SE = 0.012), 7 days post conception (Figure 1.4). However, age was not found to be a significant factor in determining if a deer performed an excursion (P = 0.125, SE = 0.378). The percentage of daily points outside the SHR had elevated values much more concentrated around conception, with a peak value of 0.057 (SE = 0.004) 1 day prior to conception (Figure 1.5).

Discussion

Our data show that changes in female behavior and space use appear to be closely linked to conception. When examining the spatial metrics relative to breeding stages, an increase in movement rate and probability of activity from prerut to rut suggests that does were actively advertising their presence during the breeding season (Sawyer 1981; Labisky and Fritzen 1998; D'Angelo et al. 2004). This is supported relative to conception by an increase in both metrics from approximately 40 days before until just prior to conception. Another indicator of the connection between female behavior and conception were the trends seen in space use. The increase in both home range and core area from prerut to rut, paired with no change in the core area:home range ratio over the same time period suggests that deer were expanding movements over a larger area while using this enlarged area in an equally uniform way (Rotem et al. 2011; Monsarrat et al. 2013). When space use was analyzed relative to days from conception, peak home range and core area sizes were observed during the period surrounding conception, suggesting that this increase is a direct result of breeding behaviors, and the peak during the rut period occurs due to most deer breeding within that window of time. Such space use is directly opposed to the behavior expected in a sit and wait strategy where deer would concentrate movement into a portion of the core area (Ivey and Causey 1981; Holzenbein and Schwede 1989; Beir and McCullogh 1990).

Perhaps the trends which most clearly demonstrate a connection between behavioral changes and breeding are the increases near the date of conception in probability of being outside the seasonal home range and the probability of an excursion near the date of conception. The probability of being outside the seasonal home range increased rapidly approaching conception, and declined abruptly post conception, suggesting that deer were attempting to increase their spatial footprint, possibly in an effort to advertise their presence to as many potential mates as possible during this brief period (Kolodzinski et al. 2010). Additionally, while the peak probability of an excursion was not until well after conception, the cluster of excursions within 3 days of conception provides further support that excursive behaviors and increases in activity prior to conception were breeding related. However, the occurrence of several excursions both before and after conception indicate that breeding is likely not the only cause of excursions, even when occurring during the breeding season. Additional explanations for such excursions could include, but are not limited to, harassment by rutting males or a response to hunting pressure (Kolodzinski et al. 2010).

The continued increases in both movement rate and probability of activity post conception were unexpected, as it is not advantageous to maintain mate seeking behavior once breeding has occurred (Labisky and Fritzen 1998). However, it is possible that a female is unaware whether she has conceived until approximately 20 days post conception, and therefore behaves as though she will be entering a second estrus. In ruminants, the body is believed to recognize pregnancy following the release of interferon tau, which signals the stoppage of luteolysis, and subsequent increase in progesterone levels (Bazer et al. 1998; Demmers et al. 1999; Spencer et al. 2004). It is likely these changes in progesterone level, referred to as the pregnancy hormone (Spencer et al. 2004), that result in behavioral changes for female white-tailed deer. Plotka et al. (1977) observed a continuous increase in progesterone levels of bred female white-tailed deer from the onset of estrus through 40 days post estrus, with a significant increase from 10 to 20 days post estrus. However, had a deer not conceived, progesterone levels would have been expected to decline beginning approximately 14 days post estrus (Plotka et al. 1977), a trend observed throughout Cervidae (Kelly et al. 1985; Chapple et al. 1993; Liu et al.

2002). We hypothesized that the maintenance of elevated levels of progesterone from days 14 - 40 post conception enable a female to identify her pregnancy and cease breeding behaviors. While this explanation corresponds with the spatial behaviors and activity levels observed in this study, additional manipulative experiments would be required to confirm this link.

Due to the moderate deer density and balanced buck:doe ratio at Brosnan Forest, previous studies would suggest that the sit and wait strategy would be the most efficient means of breeding for female white-tailed deer (Holzenbein and Schwede 1989; Labisky and Fritzen 1998). However, behavioral patterns observed during the three breeding stages closely resembled those reported by Labisky and Fritzen (1998) for a low density deer population (5 deer/km^2). As females should have experienced limited difficulty finding a mate given population dynamics at Brosnan, we must reject the conclusion of Labisky and Fritzen (1998) that excursions serve only as a last resort to find a mate. Similar to Kolodzinski et al. (2010), we conclude that excursive behavior in female white-tailed is an adaptive behavior to maximize the quality of the pool of potential mates and is an expression of female mate choice.

While it appears that female white-tailed deer are performing excursive behavior as a form of mate choice, it is not likely that these excursions are an attempt to locate a particular mate. Stopher et al. (2011) rejected the notion of does using excursions to reach preferred males in red deer as the excursions appeared random. Furthermore, as bucks are highly mobile during the rut, it has been postulated that the likelihood of an excursion allowing a doe to locate a specific male is low (Labisky and Fritzen 1998; DeYoung and Miller 2011). Instead, a straight line search, which has been observed for excursions, would maximize the likelihood of encountering any given male while an intensive search would be required to locate a particular male (Zollner and Lima 1999). This suggests that excursive behaviors may be an attempt to incite competition by alerting more males of the doe’s presence, as suggested by Cox and LeBoeuf (1977).

Our findings indicate that examining female movements relative to breeding stages provides some insight into the behavioral strategies employed by female white-tailed deer. However, examination of spatial metrics relative to an individual’s date of conception allows for a more detailed understanding of breeding behaviors. While the results of the breeding stage analysis in this study supported trends seen relative to date of conception, they failed to identify unique behaviors which provide a greater degree of insight into possible implications of animal activities. Therefore, we recommend that future behavioral studies focus on events at the individual scale as opposed to population level analyses.

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Table 1.1- Mean measures of movement rate, probability of activity during any given 30-minute interval, probability of being outside of the seasonal home range, home range size, core area size, and core area:home range ratio for female white-tailed deer at Brosnan Forest, SC during prerut, rut, and postrut periods of 2013-2015.

	Prerut				Rut				Postrut			
Metric	*n*	$\bar{x}$	S.E.	Significance[1]	*n*	$\bar{x}$	S.E.	Significance[1]	*n*	$\bar{x}$	S.E.	Significance[1]
Movement rate (m/0.5 hr)	1187	54.6	0.5	A	1375	68.0	0.5	B	1108	66.5	0.6	C
Probability of activity	48869	0.327	0.002	A	56932	0.419	0.002	B	47102	0.368	0.002	C
Probability outside SHR	52791	0.020	0.001	A	60864	0.036	0.001	B	49239	0.046	0.001	C
Home range (ha)	36	18.319	0.949	A	36	23.004	0.949	B	36	23.367	0.949	B
Core area (ha)	36	3.481	0.199	A	36	4.420	0.199	B	36	2.808	0.199	A
Core area:home range	36	0.193	0.006	A	36	0.193	0.006	A	36	0.163	0.006	B

[1] Different letters within a row indicate statistically significant differences between groups ($P < 0.05$).

Table 1.2- Deer age, date, days to conception, and breeding stage of the population for each excursion documented in adult female white-tailed deer at Brosnan Forest, SC, 2013-2015.

Deer	Age	Date	Days to conception[1]	Period
1	1.5	10/19	-4	rut
		10/26	3	rut
		11/9	17	postrut
		11/23	31	postrut
2	2.5	9/24	-3	rut
3	2.5	11/30	34	postrut
4	2.5	10/7	-1	rut
		10/8	0	rut
		10/17	9	rut
5	4.5	9/20	-43	rut
6	4.5	9/14	-23	prerut
		10/10	3	rut
		10/16	9	rut
		10/22	15	rut
		11/12	36	postrut
7	2.5	9/15	0	prerut
8	5.5	9/27	-2	rut
		10/9	10	rut

Table 1.2 - continued

Deer	Age	Date	Days to conception[1]	Period
9	2.5	10/26	-3	rut
		11/5	7	postrut
		11/25	27	postrut
10	3.5	9/30	-1	rut
11	5.5	10/31	26	postrut

[1] Negative values refer to days prior to conception and positive values refer to days post conception.

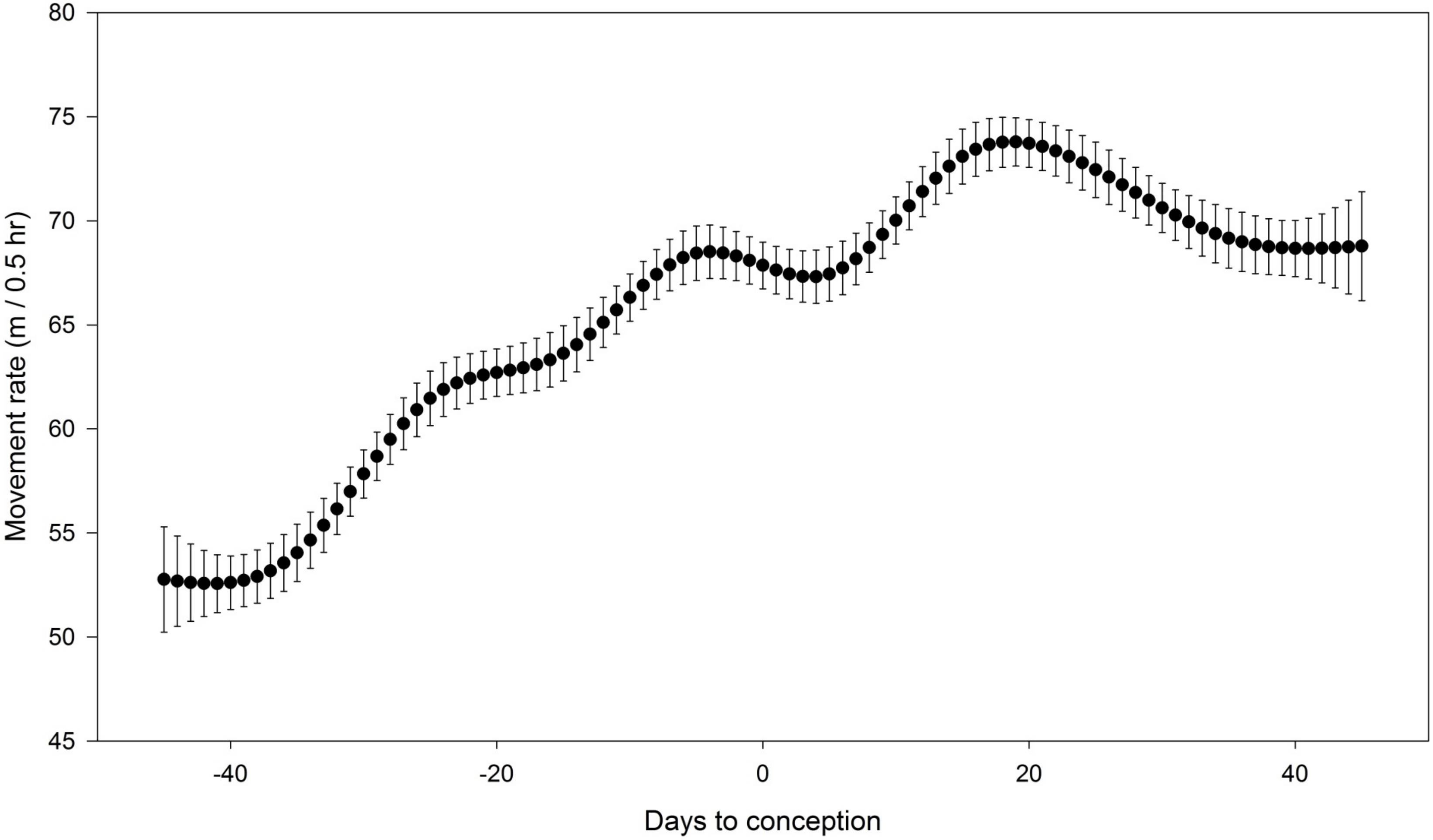

Figure 1.1 – The movement rate of female white-tailed deer at Brosnan Forest, SC relative to their date of conception, 2013-2015.

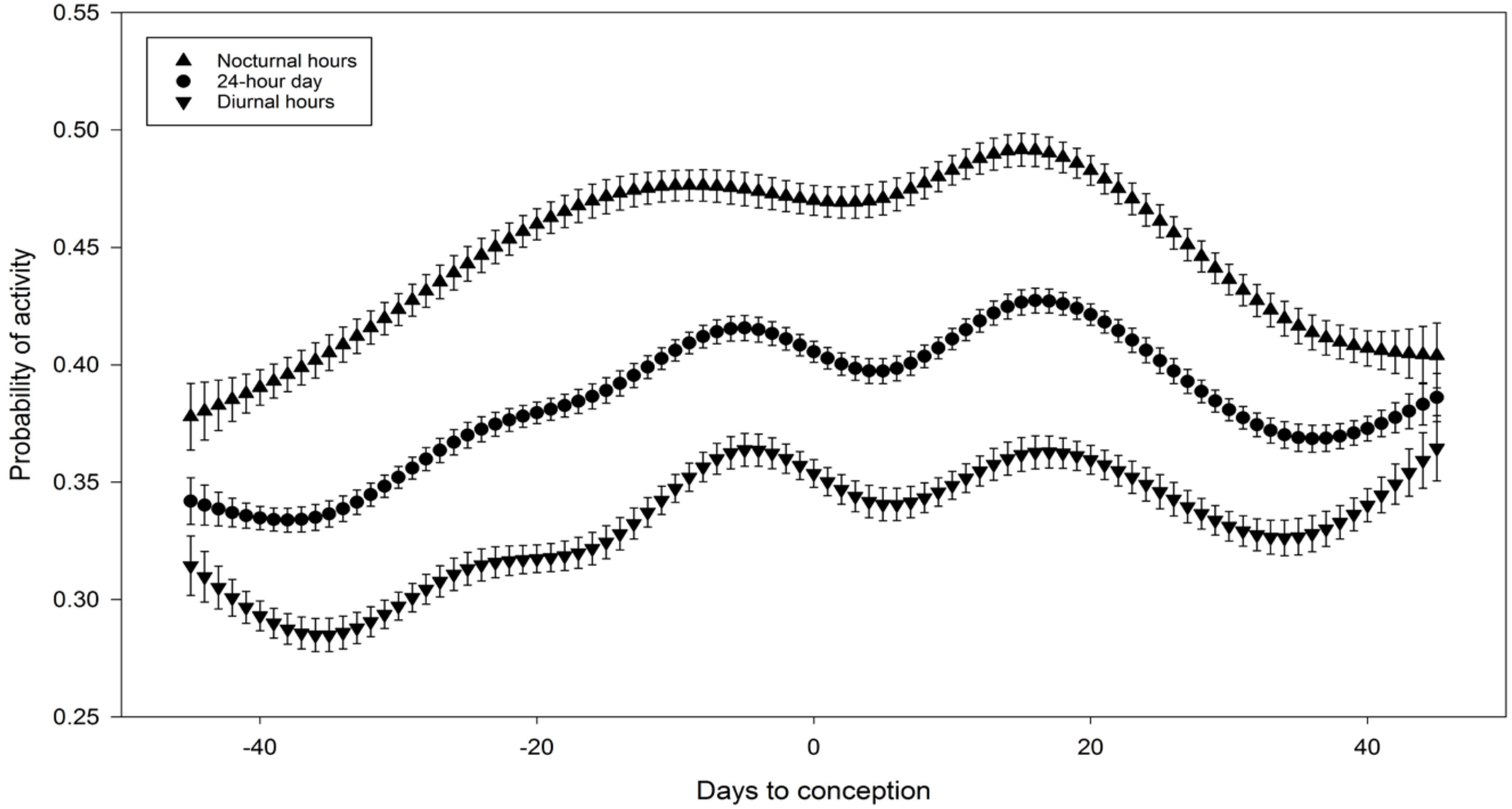

Figure 1.2 – Probability of activity during any given 30-minute interval during the 24-hour day, diurnal hours, and nocturnal hours relative to date of conception for female white-tailed deer at Brosnan Forest, SC, 2013-2015.

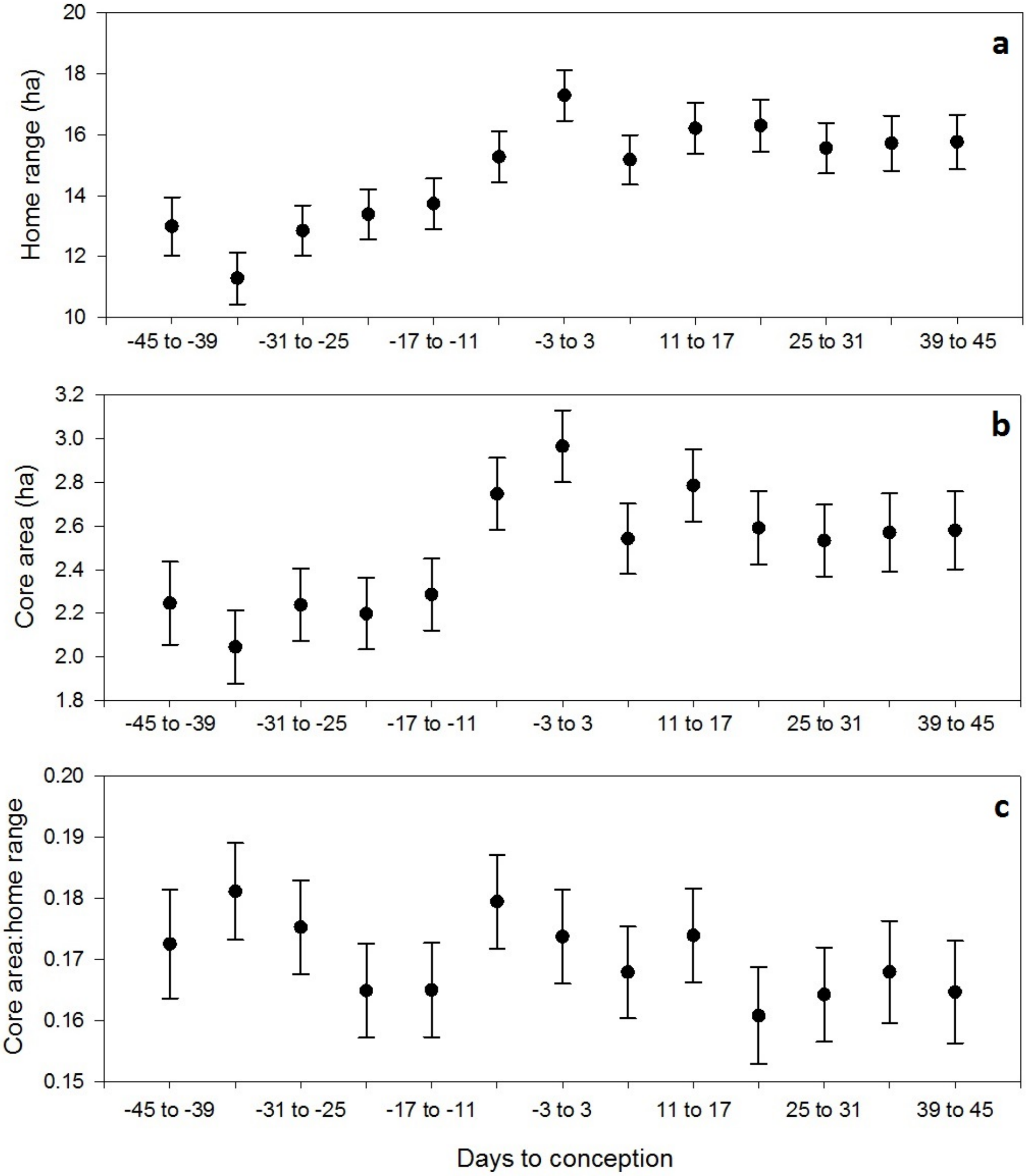

Figure 1.3 – Home range, core area, and core area:home range ratio of female white-tailed deer at Brosnan Forest, SC, on a 7-day sliding window relative to date of conception, 2013-2015.

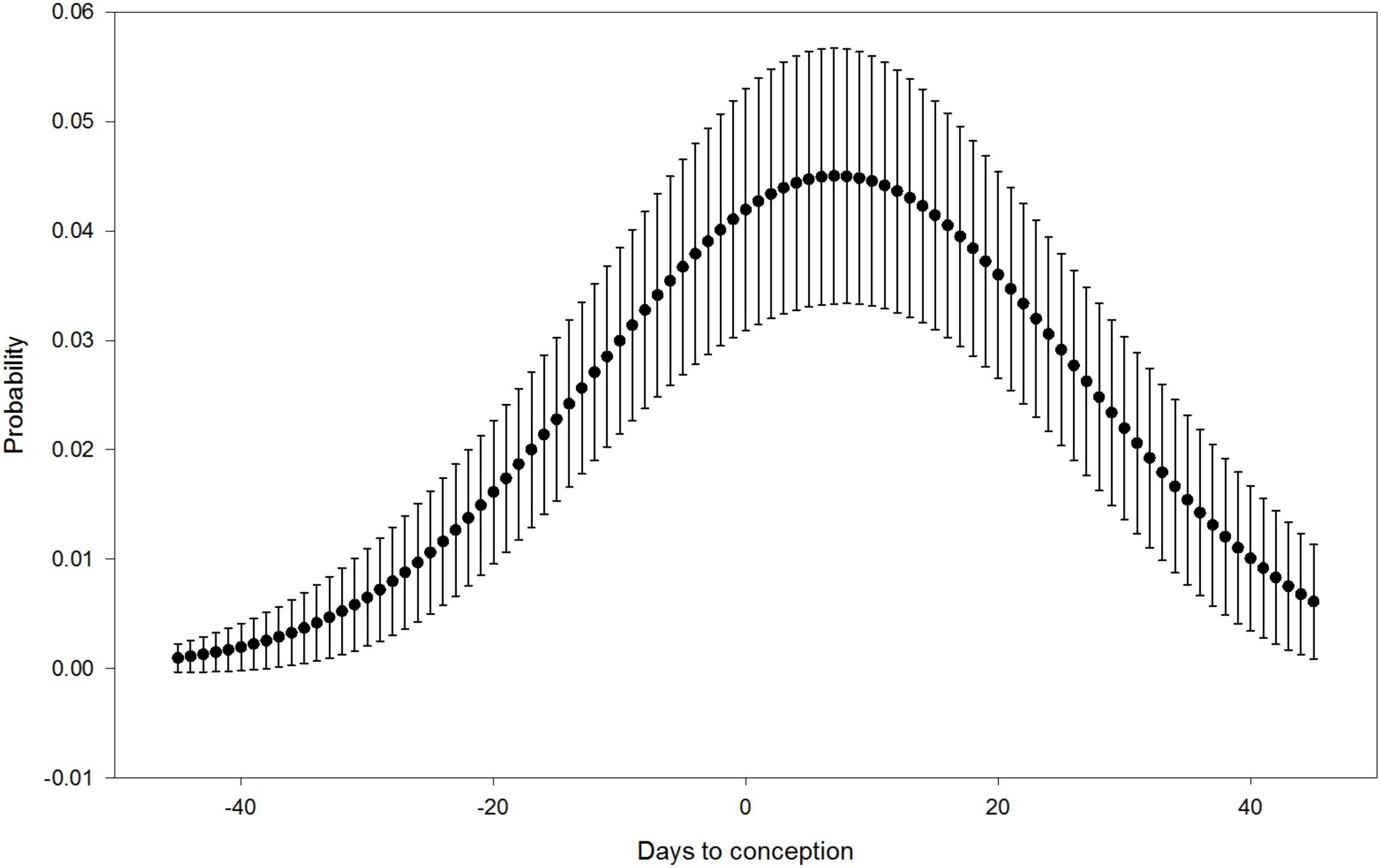

Figure 1.4 – Probability of a female white-tailed deer at Brosnan Forest, SC performing an excursion relative to date of conception, 2013-2015.

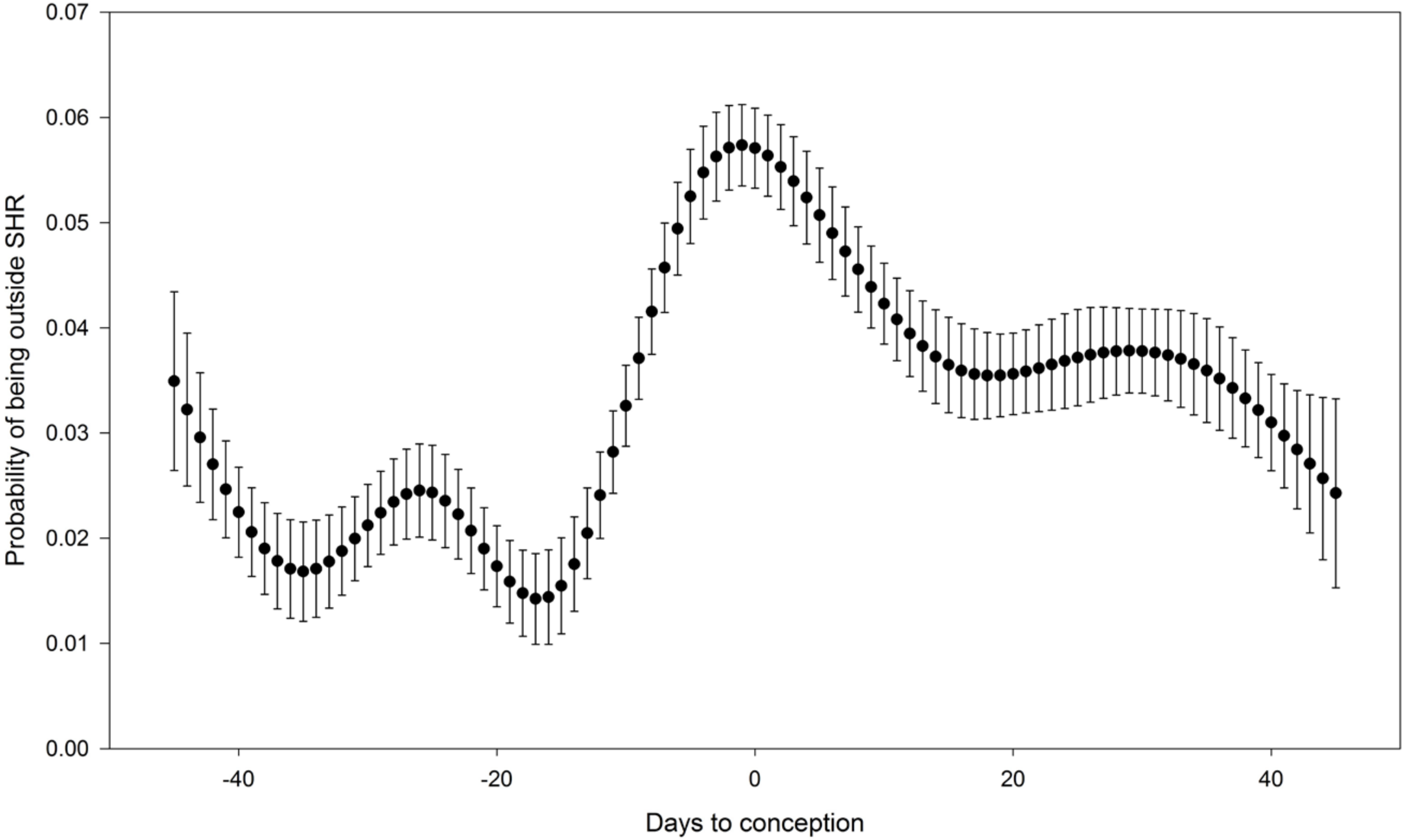

Figure 1.5 – Probability of a female white-tailed deer at Brosnan Forest, SC being outside its seasonal home range (SHR) relative to date of conception, 2013-2015.

Chapter 2: Recognizing the danger zone: female white-tailed deer alter space use in response to discrete hunting events.

Abstract

The landscape of fear theory proposes that prey should utilize habitat over space and time in a way that will minimize risk. White-tailed deer have been found to respond to temporally and spatially predictable threats posed by human hunters in a manner consistent with this theory. However, previous studies examining the response of deer to hunting have failed to account for the localized nature of risk. To determine if white-tailed deer are able to recognize and respond to risks posed by human hunters relative to specific hunting locations, we equipped 38 female white-tailed deer with GPS collars from August-December 2013-2015. Deer were generally found to increase use of feeders, food plots, and vulnerability zones during crepuscular and nocturnal periods as the hunting season progressed. However, deer use of areas around hunting stands decreased during the middle of the day and increased at night in the days immediately following a stand being hunted. We detected no change in use of areas around hunting stands during crepuscular hours in days following when a stand was hunted. Our results suggest that female white-tailed deer are able to recognize and respond to localized risks and do so with a gradient of responses based on localized risk history. However, this response was only apparent when analysis accounted for the localized nature of risk suggesting previous studies may have underestimated the ability of deer to respond to such threats.

Introduction

All prey species are faced with the challenge of continuously striking a balance between acquiring resources and minimizing risk of predation. While expressing too much caution results in nutritional deficiencies and reduced fitness, too little caution can result in injury or death (Ferrari et al. 2009, Polivka 2011). However, vulnerability to predators is often predictable, either spatially, such as how gray wolves (*Canis lupus*) are most adept at hunting in open meadows (Laundre et al. 2010), or temporally, as in the case of short-eared owls (*Asio flammeus*) being more efficient hunters on brightly illuminated nights (Clarke 1983). Predictability in predator efficiency, and thus risk of mortality, has given rise to a theory known as the landscape of fear. The landscape of fear theory combines optimal foraging theory, the risk allocation hypothesis, and game theory to propose that prey should learn from experience, and interact with their environment differently over space and time in order to minimize risk (Laundre et al. 2010). The landscape of fear theory rests upon three critical assumptions: (1) prey can learn from encounters with predators, (2) predators are not equally efficient at all times and in all habitat types, and (3) prey can identify variations in risk and will modify behavior to take advantage of them and improve fitness (Brown et al. 1999, Ferrari et al. 2009, Laundre et al. 2010).

A real world example of the landscape of fear can be seen in the response of white-tailed deer (*Odocoileus virginianus*) to pressure from human hunters. The risk deer face from human hunters is temporally predictable as hunters can only legally hunt during diurnal hours (Proffitt et al. 2009, Ciuti et al. 2012) and concentrate efforts during crepuscular periods (Proffitt et al. 2009). Hunters are also often spatially predictable as they tend to hunt from permanent stands multiple times during a season (Cromsigt et al. 2013) and concentrate near roadways (Broseth and Pedersen 2000, Stedman et al. 2004). Deer appear to recognize this predictability and react in a manner consistent with the landscape of fear, as previous studies have reported increased use of dense cover and refugia (Autry 1967, Marshall and Whittington 1969, Pilcher and Wampler 1981, Naugle et al. 1997, Kilgo et al. 1998, Kilpatrick et al. 2002; Rhoads et al. 2013), along with increased use of risky areas during non-vulnerable periods such as nocturnal hours (Kilpatrick and Lima 1999) by white-tailed deer during the hunting season. Yet white-tailed deer are not the only cervids who have been shown to recognize and respond to the predictable nature of human hunters. Similar responses have been documented in other species including elk (*Cervus elaphus*; Burcham et al. 1999, Millspaugh 2000), mule deer (*Odocoileus hemionus*; Kufeld et al. 1988), and roe deer (*Capreolus capreolus*; Bonnot et al. 2013).

While white-tailed deer appear to follow the predictions of the landscape of fear when faced with human hunting pressure, previous studies have only examined deer responses to hunting without accounting for the localized nature of the risk these hunters pose, often reporting hunting pressure for the whole landscape in hours per unit area (Autry 1967, Root et al. 1988). Though previous studies provide insight into coarse activity patterns, they ignore the possibility that animals can perceive habitats with fine spatial resolution and integrate that information into future actions. Examples of animals using fine scale spatial data to guide their movement can be seen in the annually repeated paths used by painted turtles (*Chrysemys picta*) to reach permanent water bodies following vernal draw down (Roth and Krochmal 2015), or the incorporation of high yield flowers into the "trap line" foraging of bumblebees (*Bombus terrestris*; Lihoreau et al. 2011). However, integration of fine scale spatial information into an animal's activity is not limited to instances where it enables access to high value resources. Owens (1977) reported that brant geese (*Branta bernicla*) will avoid areas in which they have recently experienced heavy disturbance and will maintain this aversion until food resources in safer areas are depleted. Similarly, the application of electrical shock has been found to successfully condition cattle against the utilization of specific areas within a homogenous pasture (Quigley et al. 1990). The avoidance of areas within which an animal has had a previously negative interaction demonstrates the ability to associate that negative experience with the specific location. Therefore, the inability of previous studies to examine the possibility of white-tailed deer recognizing the localized risk posed by hunters and responding via spatial aversion has limited researchers in our understanding of this species' ability to integrate perceived threats into their decision making process.

Obtaining information regarding the resolution with which deer perceive risk could dramatically improve our understanding of the spatial reasoning abilities of a keystone herbivore, and examining their spatial and temporal reactions to specific hunting events is the next step in advancing this knowledge. Fortunately, improvements in GPS technology now allow researchers to remotely collect detailed and precise information on animal space use and movement (Gordon 2001, Getz et al. 2007). Pairing GPS data with detailed knowledge of hunter presence would provide a unique opportunity to examine how and when deer respond to the risks posed by a predator. The goal of this study was to determine if female white-tailed deer are able to recognize and respond to the risks posed by human hunters relative to specific hunting locations. Our specific research objectives were to (1) characterize space use of female white-tailed deer relative to hunting pressure, (2) determine if female white-tailed deer recognize and respond to specific areas of risk, and (3) determine the temporal influence of risk on the space use of female white-tailed deer. As predicted by the landscape of fear hypothesis, if deer associate risk with general landscape features (hunting stands, food plots, etc.), then the likelihood of use of that resource type should decrease as the hunting season progresses (Laundre et al. 2010). However, if deer can differentiate risk between specific locations, an aversion to a resource type would not be expected, but rather they would avoid particular locations and utilize nearby alternatives.

Methods

Study Area

Our research was conducted at Brosnan Forest, a 5,830-ha tract of lower coastal plain habitat in Dorchester County, South Carolina (33.08591°N, 80.25726°W). This project took place exclusively on the 2,552-ha portion of the property located north of Highway 78. The deer density on this property has been estimated at 20/km^2 with a buck to doe ratio of 1:1.4 (J.B. Raglin, Norfolk Southern Railway, unpublished data). While the deer hunting season in this portion of South Carolina began annually on 15 August, deer hunting at Brosnan was performed in the mornings and evenings from 15 September-1 January, with guides transporting hunters to and from fixed stands that did not move within a given season. Approximately 93% forested, the study area contained mostly open longleaf pine (*Pinus palustris*) stands interspersed with mixed hardwoods (Collier et al. 2007). Hardwood drains were found throughout the property with mixed pine-hardwood areas comprised of loblolly (*Pinus taeda*), slash (*Pinus elliottii*), and pond (*Pinus serotina*) pine, along with oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Bottomland drains included oak, sweetgum, black gum (*Nyssa sylvatica*), and yellow poplar (*Liriodendron tulipifera*). The majority of forest stands were actively managed for wildlife and timber production, and burned on a 2-3 year rotation to maintain an open understory (Lauerman 2007, Collier et al. 2007). Food plots on the study area ranged in size from 0.03-8.5-ha and comprised a total of 119-ha. While a majority of plots were planted annually with a cool season mix of various clovers (*Trifolium* spp.), grains (oats, *Avena fatua*; wheat, *Triticum aestivum*), chicory (*Cichorium intybus*), and winter peas (*Pisum sativum*), additional plots received spring plantings of soybeans (*Glycine max*), sorghum (*Sorghum bicolor*), or game bird mix containing sorghum (*Sorghum bicolor*), buckwheat (*Fagopyrum* *esculentum*), benne (*Sesamum indicum*), and sunflower (*Helianthus* spp.). There were also 55 feeders distributed throughout the study area dispensing shelled corn during the hunting season.

Capture

During May-August of 2013-2015 a total of 43 female white-tailed deer (≥1 year old) were immobilized via a 2cc transmitter dart (Pneu-dart Inc., Williamsport, Pennsylvania, USA) containing a Xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 2.2 mg/kg) and Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 100mg/ml given at a rate of 4.5 mg/kg) mixture. Deer were fitted with an ATS G2110D GPS Collar (Advanced Telemetry Systems, Isanti, Minnesota) tightened to within approximately two finger widths of the neck, allowing the collar to stay in the proper upright position and improving data accuracy (D'Eon and Delaparte 2005). After processing was complete a 3-ml intramuscular injection of Tolazoline (Lloyd Laboratories, Shenandoah, Iowa; 100mg/ml given at a rate of 6.6 mg/kg) was administered to act as a reversal to the Xylazine/Telazol mixture, and deer were observed until they moved away under their own power. All protocols involving animals were approved by the Auburn University Animal Care and Use Committee (PRN# 2013-2205).

Data Collection and Manipulation

GPS collars were programmed to take fixes at 30-minute intervals from 16 August-1 December, recording position in UTM coordinates, date, time, altitude, fix status, satellites, position dilution of precision (PDOP), horizontal dilution of precision (HDOP), and temperature with each fix. Data were offloaded using ATS WinCollar software, and likely erroneous 3-dimensional fixes with PDOP > 10 or HDOP > 6, and 2-dimensional fixes with HDOP > 3 were removed (D'Eon and Delparte 2005, Lewis et al. 2007). To determine locational error, 3 collars were deployed for 5 days at the end of the research period among various habitat types found within the study site: an immature pine stand, a mature pine stand, and a mature hardwood stand. Collars were placed approximately 1-m above the ground, the neck height of a standing deer (Frair et al. 2010), with the antenna pointing directly upwards (D'Eon and Delparte 2005, Lewis et al. 2007). Coordinates for the deployment locations were taken with a Trimble GeoXT GPS unit, with all locations accurate to within one meter. As all collars were of the same model, the assumption was made that each collar had comparable precision, and that any variance between collars was habitat driven (Lewis et al. 2007). The Euclidean distance of each fix from its corresponding known location was calculated to provide mean locational error ($\bar{x}$ = 12.945 m, SD = 9.806 m).

Following the data acquisition method of Webb et al. (2010), the times of sunrise and sunset were downloaded from the naval observatory website for Summerville, South Carolina (~33 km from the study site). Each fix was then categorized according to the time of day which was represented by 3 periods: DAY-HUNTING, DAY-NONHUNTING, and NIGHT. DAY-HUNTING ranged from one half hour before sunrise until eight in the morning and from three in the afternoon until one half hour after sunset, while DAY-NONHUNTING was from eight in the morning until three in the afternoon. These times were determined based upon when hunters were removed from stands in the morning and delivered to stands in the evening, such that DAY-HUNTING represents times when hunters would be in stands, and DAY-NONHUNTING represents times when stands would be empty. NIGHT ranged from one half hour after sunset until one half hour before sunrise. The number of days since the beginning of the hunting season was also recorded for each fix.

We identified 3 features of the study site (automatic broadcast feeders, food plots, and hunting stands) around which we hypothesized deer would change usage patterns relative to their perception of risk. The location of each feeder on the study site was recorded, and a buffer with a radius of 50 meters (McCracken et al. 1998, Cederholm 2012), was then applied via the ArcGIS buffer tool (v 10.2; ESRI 2013). Similarly, the location of each food plot was documented, and the shape of each was individually digitized. Finally, the location of each hunting stand was recorded, and a vulnerability zone around the stand, depicting areas in which deer were vulnerable to hunters ($\leq$ 200 meters from the stand), was digitized. The vulnerability zone was set by sitting in the stand prior to the beginning of the hunting season and using a laser rangefinder to determine the area in all directions within which a deer would be visible to the hunter. Measurements were recorded prior to the beginning of the hunting season to serve as a conservative estimate, since the loss of foliage during winter would expand the area in which the deer was vulnerable. While previous work represented vulnerability zones by setting a uniform buffer around each stand (Karns et al. 2012), we believe that our approach more realistically represented the risk experienced by an animal as changes in vegetation impact the ability of a hunter to detect deer around a stand. Each fix was then classified as being within or not within a feeder area, a food plot, or a vulnerability zone around a stand. Classifications were made independently and were not mutually exclusive, as the vulnerability zone around a stand could have, but may not have, included a food plot, feeder, or both. We assumed that as the hunting season progresses decreases in the use of these areas would suggest an aversion due to perceived risk, while an increase would suggest a draw to the available resources (Owens 1977).

In order to quantify changes in activity throughout the season, movement rate was calculated by finding the average Euclidean distance between consecutive half hour fixes throughout each time period per deer per day (Root et al. 1988, Labisky and Fritzen 1998, Webb et al. 2010, Rhoads et al. 2013). Similar to the censoring method applied by Webb et al. (2010), only daily periods with at least half of the possible consecutive fixes were utilized. The data derived by this metric provides insight into the degree of activity displayed by the animal, and can be interpreted as a measure of response to hunters (Roseberry and Klimstra 1974, Karns et al. 2012). Previous studies have hypothesized that increased movement during periods of hunting pressure result from deer increasing interpatch movement in an effort to avoid hunters, especially in habitats with limited cover (Marshall and Whittington 1969, Root et al. 1988, Rhoads et al. 2013). Movement rate is also widely used in the deer literature and allows for the comparison of results between studies (Root 1998, Kilpatrick and Lima 1999, Karns et al. 2012, Rhoads et al. 2013).

Since all hunters were delivered to and picked up from their hunting stand by a guide, daily records were maintained recording which stands were hunted. The nearest stand was determined for each fix via the NEAR tool in ArcGIS (v 10.2; ESRI 2013), and the time since hunted, measured in 24 hour increments ranging from hunted within the past 24 hours through not hunted within the past 169 hours, was recorded. The number of hunting events that had previously occurred at the nearest stand was also recorded for each fix. Changes in the use of the vulnerability zone around a stand following a hunting event demonstrate how deer respond to localized risk, as such changes account for aversion of a single location. Furthermore, the length of time that an animal maintains their aversion toward an area of risk provides insight into the degree of fear the animal has to the experienced risks (Fagan et al. 2013).

Data Analysis

The likelihoods of a deer utilizing a feeder, food plot, and the vulnerability zone around a stand during the DAY-HUNTING, DAY-NONHUNTING, and NIGHT periods were each calculated as a function of the number of days since the beginning of hunting season using logistic regression. The random effect of deer was applied, along with a random effect for the nearest feeder, food plot, or vulnerability zone. Beta estimates were exponentiated to the 77th power to determine the comparative likelihood of use on the 77th day of hunting as compared to on day 0. The 77th day was used as this corresponded with our final day of data collection. Probability of use was predicted from the statistical model for feeders, food plots, and vulnerability zones around stands during each period on days 0, 38, and 77 of the hunting season. Days 0, 38, and 77 represent the beginning, midpoint, and end of hunting, respectively. Movement rate as a function of days since the beginning of hunting season was also calculated for each time period using linear regression.

The likelihood of a deer utilizing the vulnerability zone around a stand as a function of time since hunted, the number of hunting events to date, the number of days since the beginning of the season, and the interaction between time since hunted and number of hunting events to date was analyzed for each of the 3 time periods via logistic regression. Random effects for deer and the nearest vulnerability zone were applied. The probability of a deer utilizing the vulnerability zone around a stand was predicted from the statistical model. All analyses were conducted in R (v3.1.3; R Core Development Team 2015).

Results

During the course of the study, 2 deer died prior to the beginning of the study period, 2 collars malfunctioned, and 1 collar was unable to be recovered at the time of data analysis, leaving a total of 38 deer. These 38 collars had an average fix success rate, after data censoring, of 87.36% (n = 172,069) while the stationary collars had an average fix success rate of 99.87% (n = 792).

When space use was examined without accounting for the localized nature of risk, number of days since the beginning of hunting was found to significantly impact ($P < 0.001$) the likelihood of a deer utilizing feeders, food plots, and vulnerability zones around stands during the DAY-HUNTING and NIGHT periods, with likelihood of use increasing each additional day since the beginning of the season (Figure 2.1). During the DAY-NONHUNTING period, deer did not significantly alter their usage of feeders (0.786 times as likely, P = 0.203, CI = 0.539-1.147) as the hunting season progressed, but were 0.641 times as likely ($P \leq 0.001$, CI =0.530-0.775) to utilize the vulnerability zone around a stand, and 2.367 times as likely ($P \leq 0.001$, CI = 1.787-3.136) to use a food plot on day 77 of hunting as on day 0. On day 0 of the hunting season deer moved an average of 65.3 (SE = 1.5), 40.7 (SE = 1.2), and 80.0 m/0.5-hr (SE = 1.2) during the DAY-HUNTING, DAY-NONHUNTING, and NIGHT periods, respectively. Movement rate during the DAY-HUNTING period increased by 0.16 m/0.5-hr ($P < 0.001$, SE = 0.033) with each additional day of hunting. The increase in movement rate equates to an additional 24.64 m/hr during hunting hours on the 77th day of hunting as compared to day 0. Movement rates during the DAY-NONHUNTING (0.04 m/0.5-hr; P = 0.143, SE = 0.028) and NIGHT (-0.04 m/0.5-hr, P = 0.148, SE = 0.026) periods did not change with each additional day of hunting.

When use of vulnerability zones around stands was examined as a function of localized risk, different trends emerged from those seen when localized risk was not taken into account. Deer did not change their usage of vulnerability zones around a stand during the DAY-HUNTING period (Figure 2.2) following additional time since being hunted (1.002 times as likely, P = 0.876, CI = 0.971-1.035) or additional hunting events to date (0.976 times as likely, P = 0.373, CI = 0.924-1.031). No significant interaction was found between these two factors (P = 0.284, SE = 0.004). However, during the DAY-NONHUNTING period deer were 1.010 times as likely ($P < 0.001$, CI = 1.045-1.149) to utilize the vulnerability zone around a stand following each additional 24 hour period after a hunting event, but did not significantly alter usage following additional hunting events (0.994 times as likely, P = 0.880, CI = 0.917-1.077; Figure 2.3). The interaction between time since hunted and number of hunting events was not found to be significant (P = 0.358). During the NIGHT period the likelihood of a deer utilizing the vulnerability zone around a stand was greatest immediately following the first hunting event, and decreased with each subsequent 24 hour period after the hunting event ($P < 0.001$, Figure 2.4). However, this relationship changed following a 4th hunting event, due to a significant interaction ($P < 0.001$) between time since hunted and number of hunting events, such that the likelihood of use was least immediately following the hunting event and increased with each subsequent 24 hour period post hunt.

Discussion

Our data show that female white-tailed deer have the capacity to recognize and respond to localized threats posed by human hunters through altered behavior and space use. However, this response was not readily apparent when we did not account for the localized nature of risk. The increased use of feeders, food plots, and vulnerability zones around stands during the DAY-HUNTING period suggests that the level of hunting pressure was not sufficient to cause deer to avoid these areas ubiquitously across the landscape, which would be the expected response under the landscape of fear hypothesis. This conclusion is supported by a common belief that there is a minimum threshold of hunting pressure which must be met before deer will adjust behaviors to a degree that is observable at the population level (Marshall and Whittington 1968, Root et al. 1988, Karns et al. 2012). An example of this was reported by Karns et al. (2012), who concluded that a lack of change in male white-tailed deer space use from pre hunting to hunting periods, as measured by home range size, core area size, and use of areas surrounding hunting stands, was due to hunting pressure being of insufficient intensity to alter behavior. A similar conclusion was described by Neumann et al. (2009) when they reported a lack of change in moose (*Alces alces*) behavior during a low pressure hunting period. We believe that increased use of feeders, food plots, and vulnerability zones around hunting stands as the season progressed was likely due to deer seeking the food resources these areas provided as native vegetation became less abundant and less palatable during the fall and winter months (Crawford 1982, Johnson et al. 1987). We concurrently observed a general increase in movement rate across the population as the season progressed. As the understory at this site was generally open, such a response would be expected (Marshall and Whittington 1969, Root et al. 1988, Rhoads et al. 2013) as increased movement allowed the animal to move between resource patches, thereby avoiding perceived risks while still accessing high value resources. However, some argue that increased movement raises a deer's likelihood of encountering a hunter and thereby further increases risk (Roseberry and Klimstra 1974, Karns et al. 2012).

Hunting season length likely influences how deer respond to risks posed by hunters, due to the tradeoff between nutritional demands and risk avoidance (Lima and Bednekoff 1999, Ferrari et al. 2009). When risk is short lived any negative effects on fitness due to reduced food access are likely negligible. However, as the duration of risk extends, as would be expected in areas that have hunting seasons that last for several months, the negative effects on fitness due to undernutrition increase and animals should be more likely to engage in risky behavior (Lima and Dill 1989, Ferrari et al. 2009). White-tailed deer have been found to avoid previously preferred habitats such as clear cuts, young pine plantations, and other open habitats during periods of brief hunting pressure (Kilgo et al. 1998). However, in this study, hunting was sustained over several months, suggesting that the nutritional demands experienced by deer throughout the fall could outweigh the risks associated with hunting pressure and drive the behavior we observed when examining space use without accounting for the localized nature of risk (Lima and Bednekoff 1999, Ferrari et al. 2009).

Our data suggest that deer were able to detect hunting pressure and temporally shifted their space use to account for the elevated risk associated with hunting events. An example of this can be seen during the NIGHT period when our study animals responded to the initial hunting events by increasing use of that location during nocturnal hours following the event. We had expected this temporal response to risk, as similar patterns have been documented previously, where deer were found to increase activity during nocturnal hours as a result of hunting pressure (Kilgo et al. 1998, Webb et al. 2010, Karns et al. 2012). Lima and Dill (1989) explained this temporal shift in space use as a strategy by which to reduce the likelihood of encountering risk, as it takes advantage of the temporally predictable nature of hunters. Such a response makes sense when deer recognize risk as temporally restricted, because it enables them to minimize risk while remaining within a known area and continuing to utilize a high value resource. Yet, a different response is observed following the fourth time a stand was hunted, where deer displayed the least probability of use the night following the hunting event and increased use thereafter. This is a fundamentally different response from what was observed during the nights following the first time a stand was hunted, and we interpret this as suggesting that white-tailed deer rely on past experiences to choose between multiple response options after encountering risk. This change in how deer respond to localized risk as a result of the number of times a stand is hunted suggests that white-tailed deer are capable of recognizing localized risks from human hunters, storing and modifying this information following additional experiences, and utilizing this cumulative knowledge to minimize risk. However, antipredator behaviors are costly to maintain, and the strength of aversion should reduce over time if risks are no longer encountered (Blumstein 2006, Stankowich and Coss 2007).

We had expected deer to change their use of stands during their most vulnerable time (DAY-HUNTING). However, the trends observed during this period were not found to be significant, possibly because this period serves as an important feeding window for white-tailed deer (Montgomery 1963, Rouleau 2002). The length of the hunting season at our study area may cause aversion during this window to be unfeasible as it would reduce access to the high value resource areas associated with hunting stands. While the number of times hunted to date lacked a significant effect during both DAY-HUNTING and DAY NONHUNTING, and time since hunted was not significant during the DAY-HUNTING period, the trends observed do provide an additional indication that deer can perceive the risk posed by human hunters and will alter their space use in an effort to minimize risk. It is important to recognize that decreased use of vulnerability zones around occupied hunting stands is different than avoidance due to prior experience. Avoidance of an area the day of hunting is expected (Behrend and Lubeck 1968, Stankowich 2008) and likely indicates detection of the hunter via visual, olfactory, or auditory clues. Conversely, avoiding an area for a length of time greater than the initial exposure demonstrates the ability to, for at least some period of time, create a spatial map of risk and react accordingly (Fagan et al. 2013). Furthermore, the reduction in probability of use with each additional time a stand was hunted suggests that deer recognize a gradient of risk, as opposed to viewing areas as either risky or non-risky (Ferrari et al. 2009). By increasing the strength of the reaction following subsequent hunting events, deer are demonstrating an accumulation of knowledge about the previous risks at specific locations.

The observation of temporary aversion to the vulnerability zone around a hunting stand after that stand had been hunted suggests that low levels of hunting pressure, though previously believed to be non-disruptive (Marshall and Whittington 1968, Root et al. 1988, Karns et al. 2012), do indeed impact deer behavior. However, such impacts are visible only when the localized nature of risk is taken into account. Therefore, previous studies which focused on patterns of space use without accounting for the localized nature of risk likely failed to identify spatially discrete responses, and thus underrepresented risk detection and avoidance abilities of white-tailed deer. For example, Karns et al. (2012) reported that male white-tailed deer utilized areas surrounding permanent deer stands equally during hunting and non-hunting periods for all times of day. These results are similar to our findings that use of high risk areas during hunting hours increased throughout the hunting season. Only by accounting for the temporal nature of risk associated with areas of vulnerability was it possible for us to detect the aversive behaviors of white-tailed deer.

Our findings indicate that white-tailed deer are capable of recognizing and responding to localized risks, suggesting that even limited hunting pressure can impact space use patterns of large cervids. With this approach now established, white-tailed deer can serve as a unique model through which the response of wild cervids to localized risks across gradients of intensity and duration can be examined. This is possible because deer are heavily hunted and the considerable potential to document risk by monitoring hunters. Gaining insight into the role such factors play in the response of white-tailed deer to localized risks will further our understanding of the cognitive processes of large herbivores, as well as provide an indication of what responses can be expected in the face of changing ecosystems. The need for additional research notwithstanding, these results can be taken to suggest that low levels of human disturbance impact animal behaviors (Ditchkoff et al. 2006), and that, instead of attempting to determine if anthropogenic disturbances impact a given species, scientists and policy makers would be better served by looking to understand if the behavioral changes displayed post-disturbance are of biological significance.

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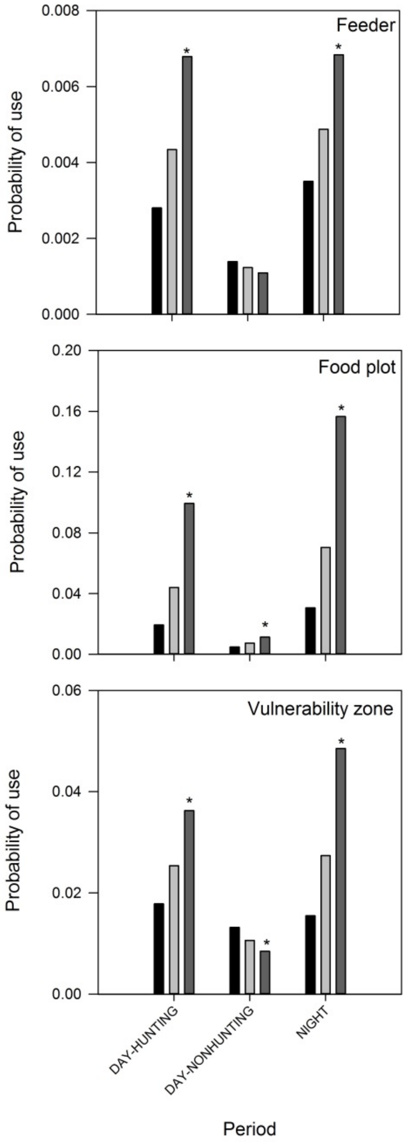

Figure 2.1 – The probability of a female white-tailed deer utilizing a feeder, food plot, or the vulnerability zones around hunting stands at Brosnan Forest, SC during any given half hour interval of the DAY-HUNTING, DAY-NONHUNTING, and NIGHT periods on days 0 (leftmost bars), 38 (middle bars), and 77 (rightmost bars) of the hunting season, 2013-2015. Asterisks (*) denote models in which the number of days from the start of the hunting season was found to significantly impact use of the resource area ($P \leq 0.05$).

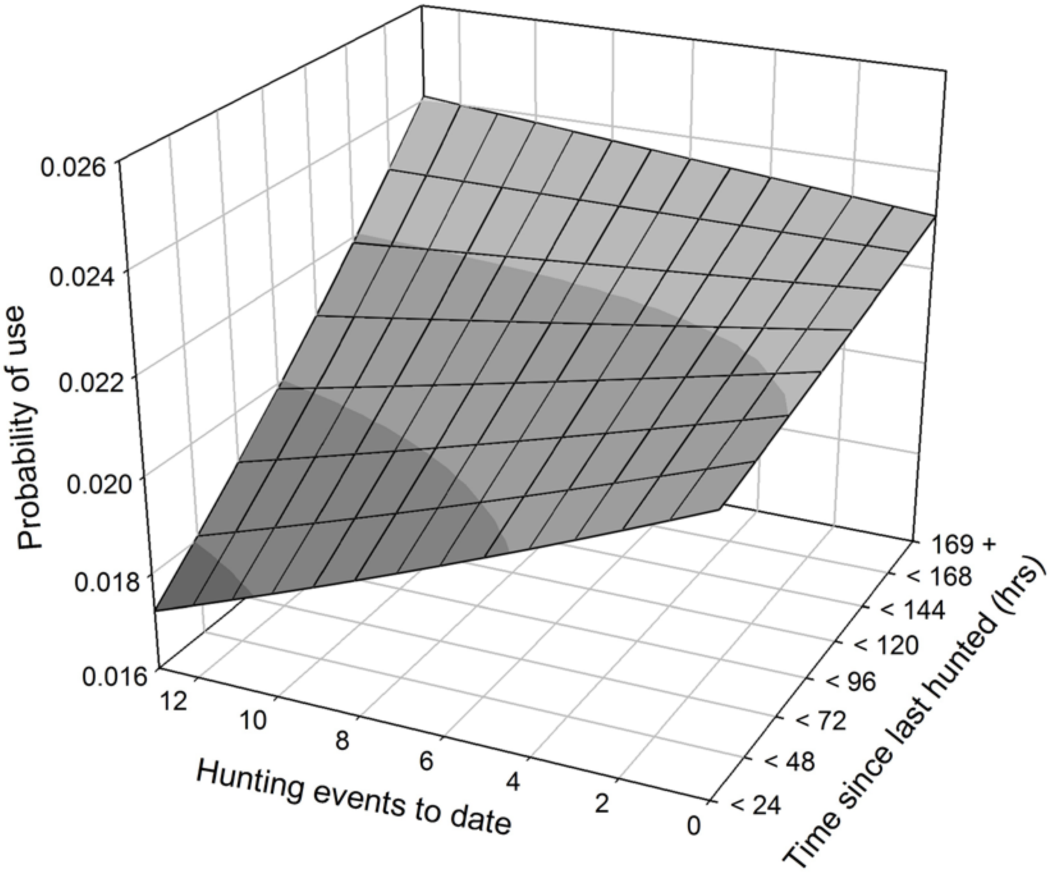

Figure 2.2 – The probability of a female white-tailed deer at Brosnan Forest, SC utilizing the vulnerability zone around a hunting stand during the DAY-HUNTING period on the 77th day of the hunting season as a function of the time since that stand had been hunted, the number of hunting events at that stand to date, and the interaction between these two variables, 2013-2015.

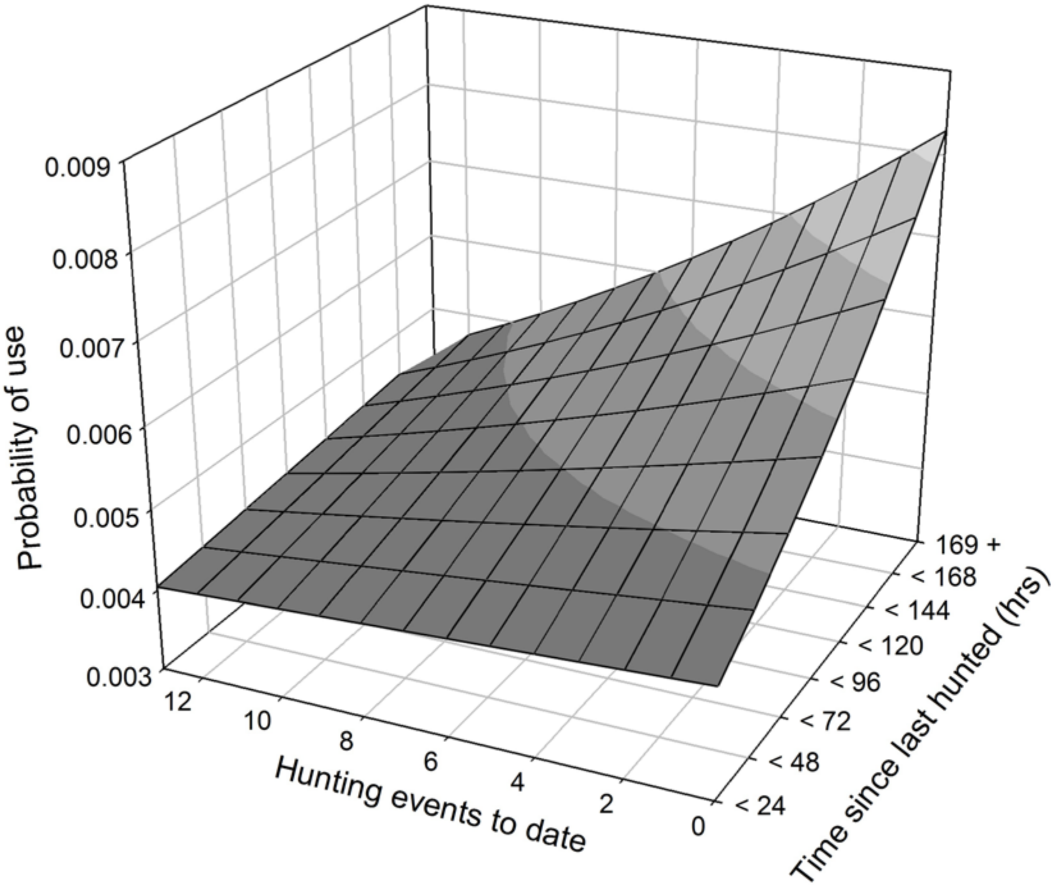

Figure 2.3 – The probability of a female white-tailed deer at Brosnan Forest, SC utilizing the vulnerability zone around a hunting stand during the DAY-NONHUNTING period on the 77th day of the hunting season as a function of the time since that stand had been hunted, the number of hunting events at that stand to date, and the interaction between these two variables, 2013-2015.

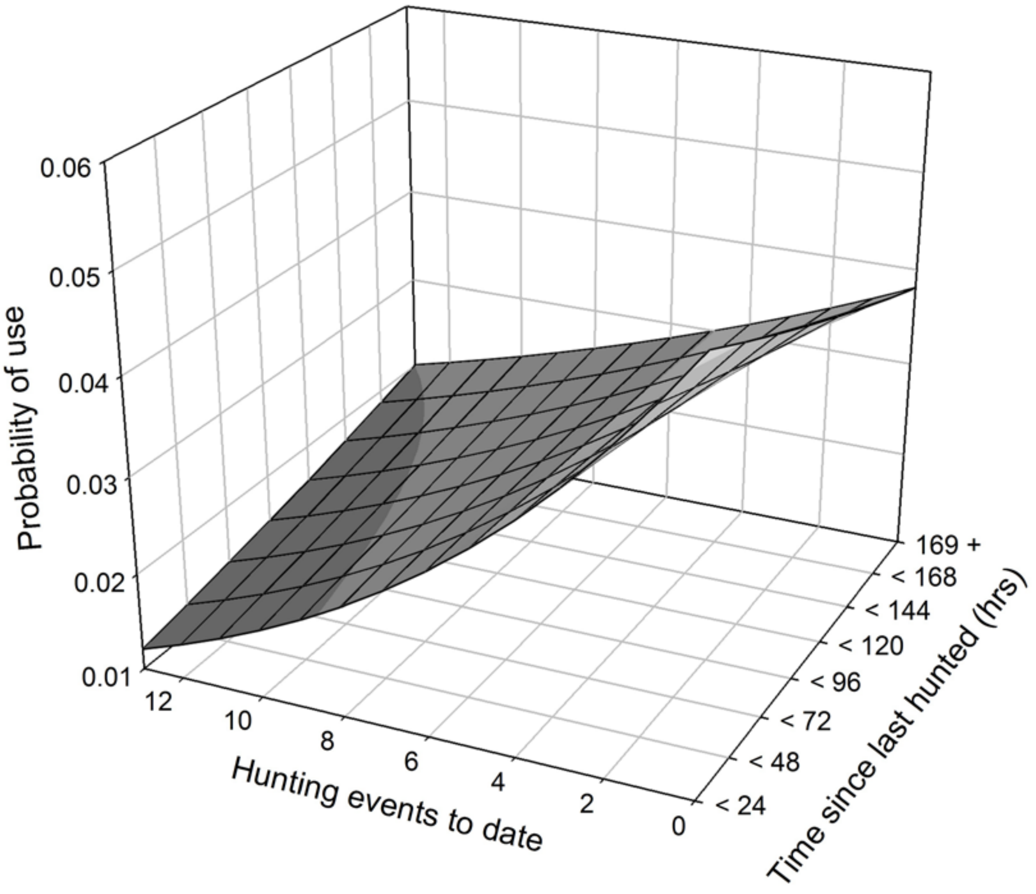

Figure 2.4 – The probability of a female white-tailed deer at Brosnan Forest, SC utilizing the vulnerability zone around a hunting stand during the NIGHT period on the 77th day of the hunting season as a function of the time since that stand had been hunted, the number of hunting events at that stand to date, and the interaction between these two variables, 2013-2015.