Effects of Abiotic Factors on White-tailed Deer Activity in South Carolina

by

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Abstract

A myriad of internal and external factors continuously influence behavior of all animals. One group of environmental factors, abiotic factors (e.g., wind, temperature, and moon phase), are continuously present and constantly changing in the environment of all animals. Actions animals take in response to abiotic factors have the potential to affect their survival and lifetime fitness. Measuring behavioral responses to abiotic factors is an important step in understanding how animals interact with their environment. To investigate how white-tailed deer (*Odocoileus virginianus*) in the Southeast interact with their environment, we affixed GPS collars to adult deer and modeled movement relative to abiotic factors. We observed that weather condition, temperature, wind speed, barometric pressure, moon phase, moon position, and nocturnal brightness affected activity in some seasons and times of day. Responses to abiotic factors were typically less pronounced than circadian fluctuations in activity, and occurred most often during non-peak times of activity.

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Chapter 1: Brightness and wind speed influence nocturnal activity of white-tailed deer (*Odocoileus virginianus*)

Abstract

Animal behavior is continuously influenced by both factors and abiotic factors. Abiotic factors, such as nocturnal brightness and wind speed, can affect mammalian distance senses (i.e., vision, olfaction, and hearing), and thus the ability of prey species to detect and avoid predators. Impaired predator detection and avoidance may cause deer to temporally adjust activity to avoid riskier nocturnal periods. Likewise prey species may take advantage of periods that allow for increased predator detection or foraging efficiency by increasing activity. Accordingly, we examined the influence of nighttime brightness and wind speed on activity of white-tailed deer (*Odocoileus virginianus*). We captured and GPS-collared 116 adult (both male and female) white-tailed deer from 2009-2018 in South Carolina, USA. To assess whether deer responded to these abiotic factors, we created a nocturnal brightness index and analyzed deer activity relative to nocturnal brightness and wind speed data collected near the study site. Our data suggested that probability of activity increased with increasing nocturnal brightness for both sexes; however, the relationship was more pronounced in females. Additionally, female activity decreased with increasing wind speed. The interactive effect of brightness and wind speed was greater in females than males, with females decreasing activity as wind speed increased under darker conditions, and increasing activity as wind speed increased under brighter conditions. Female deer were generally more responsive to changes in both nocturnal brightness and wind speed, suggesting that changes in predation risk associated with nocturnal brightness and wind speed are greater for females than males. The activity responses to brightness and wind speed observed here deviate from the majority of research on nocturnal activity, which has typically

been conducted on small mammalian species, and likely differs due to differing life history constraints between these species and white-tailed deer. The changes we observed in nighttime activity suggest that deer adjust activity according to nocturnal risk, however changes in nocturnal activity observed here are of smaller magnitude than changes in activity throughout the diel period, suggesting that daily endogenous rhythms have a stronger influence on activity.

Introduction

A myriad of internal (nutritional condition, physiological state, etc.) and external factors (predation risk, climate, moon phase, access to resources, etc.) act in conjunction to continuously influence behavior of all animal species, and the specific actions animals take in response to these factors have the potential to affect their survival and lifetime fitness. One such aspect is predator avoidance behavior, and it has been widely demonstrated that prey species alter activity patterns (Kramer and Birney 2001, Middleton et al. 2013, Pratas-Santiago et al. 2017, Wiskirchen 2017), spatial dynamics (White et al. 2014, Owen-Smith and Traill 2017, Kohl et al. 2018), and habitat selection (Gigliotti and Diefenbach 2018) to avoid predators and reduce risk of predation. For example, Hebblewhite and Merrill (2007) reported that both migratory and non-migratory elk (*Cervus canadensis*) were able to avoid high risk areas associated with wolves (*Canis lupus*) by altering their use of space. Migrants reduced risk by moving to areas with decreased predation risk, and non-migrants reduced risk by using areas within their home range that wolves tended to avoid. Similarly, some species are able to reduce risk of predation by altering their behavior temporally. For example, both *Daphnia* spp. (Stich and Lampert 1981) and African buffalo (*Syncerus caffer*; Valix et al. 2009) temporally shift their use of resources to avoid times of day when they are most likely to encounter predators.

While predator-prey dynamics are often described using temporal or spatial shifts in

activity/behavior, a variety of other factors can interact with space and time to influence

predator-prey interactions. For example, abiotic conditions can influence the ability of prey

species to detect predators (Leuthold 1977, Cherry and Barton 2017), and likewise, abiotic

factors can influence the hunting efficiency of predators (Wells 1978, Wells and Lehner 1978,

Stander 1992, Stander and Albon 1993, Cherry and Barton 2017). Much of the research that has

been conducted in this area has been with smaller mammals (e.g., Bowers 1988, Gilbert and

Boutin 1991, Julien-Laferrière 1997, Gigliotti and Diefenbach 2018). Doucet and Bider (1974)

found that masked shrews (*Sorex cinereus cinereus*) were more active on cloudy compared to

clear nights, and Orrock et al. (2004) observed that oldfield mice (*Peromyscus polionotus*)

altered foraging due to indirect cues of predation (precipitation and moon illumination) by

increasing foraging on nights when rain was falling and decreasing foraging activity on brighter

nights. However, because small and large mammals often differ in life history strategy (e.g., R-

versus K-selected), the fitness consequences of adjusting behavior due to abiotic factors likely

differ. Accordingly, in contrast to masked shrews and oldfield mice, Kufeld et al. (1988) found

no relationship between cloud cover and nighttime feeding or resting behavior of mule deer

(*Odocoileus hemionus*).

White-tailed deer (*Odocoileus virginianus*) are a large mammalian ruminant that inhabit

much of North and South America (Hefflefinger 2011), and are the most economically important

game species in the United States (Allen et al. 2013, U.S. Department of the Interior 2014).

Consequently, there is widespread interest in deer ecology and factors that affect their behavior,

which has yielded a large body of knowledge, and numerous studies have specifically examined

deer behavior in the context of predation. In the southeastern United States, hunters are the

leading source of mortality for adult white-tailed deer (Ditchkoff et al. 2001, Webb et al. 2010,

Collins and Kays 2011, Wiskirchen 2017), and recent research suggests that white-tailed deer can recognize and respond to risk associated with human hunters (Little et al. 2014, Sullivan et al. 2018). Predators present in this region can impact deer populations as well (Kilgo et al. 2010, Kilgo et al 2012), but tend to influence fawn survival (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, McCoy et al. 2013, Nelson et al. 2015) more than survival of adult deer (Labisky and Boulay 1998, Kilgo et al. 2016). Nevertheless, some adult deer mortality is attributed to bobcats (*Lynx rufus*; Labisky and Boulay 1998) and coyotes (*Canis latrans*; Chitwood et al. 2014, Kilgo et al. 2016) in the southeastern United States, and adult deer may respond behaviorally to risk associated with these predators. Recent work suggests that adult deer vigilance during foraging activity increases with coyote presence (Cherry et al. 2015) and increasing coyote abundance (Gulsby et al. 2018). Seasonal differences also appear to play a role in the predation risk/foraging tradeoff, with females being more sensitive to risk associated with coyotes during fall when fawns are vulnerable to predation, and males more sensitive during winter when they are recovering from the breeding season (Cherry et al. 2015, Gulsby et al. 2018). Understanding how deer respond to predation risk, as influenced by abiotic factors, would improve our understanding of how large mammals alter their behavior to increase their chances of survival. Additionally, white-tailed deer may act as a more appropriate model species than the typical small mammalian model species when considering the behavioral consequences of risks associated with abiotic factors in other large mammals.

We examined the influence of abiotic factors on nighttime activity patterns of white-tailed deer to improve our understanding of how large mammals alter behavior to reduce risk of predation. Moonlight intensity and wind speed can affect visual, auditory, and olfactory conditions at night (Wells 1978, Ruzicka and Conover 2011, Prugh and Golden 2014, Cherry

and Barton 2017) and subsequently the ability of predators and prey to detect each other (Sauer 1984, D'Angelo et al. 2008, Ditchkoff 2011), potentially influencing activity decisions. Accordingly, our objective was to determine whether nighttime brightness and wind speed influenced activity of white-tailed deer. We hypothesized that deer would be less active on nights that are brighter and less windy because that is when predators' senses help them hunt at night most efficiently, and we expected females to show a more prominent response to these abiotic conditions compared to males because females and their fawns are predated upon more often than males in the Southeast.

Methods

Study Area

Our study took place on Brosnan Forest, a 5,830-ha tract of land owned by Norfolk Southern Railway, located in Dorchester County, South Carolina. Mature, longleaf pine (*Pinus palustris*) stands comprised the majority of the forested area on the property. The remaining areas consisted of mixed pine-hardwood stands comprised of loblolly (*P. taeda*), slash (*P. elliottii*), and pond (*P. serotina*) pines, oak (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Drainages were dominated by hardwood species including oak, sweetgum, black gum (*Nyssa sylvatica*), and yellow poplar (*Liriodendron tulipifera*). The majority of Brosnan Forest was burned on a 2-3 year rotation to maintain an open understory (Lauerman 2007; Collier et al. 2007). A total of 126 ha of small food plots containing clover (*Trifolium* spp.), oats (*Avena sativa*), wheat (*Triticum aestivum*), rye (*Secale cereale*), chicory (*Cichorium intybus*), soybeans (*Glycine max*), and winter peas (*Pisum sativum*) were planted annually throughout the study area (McCoy et al. 2013). Additionally, supplemental corn and

protein feeders were distributed throughout the study area at a density of approximately 1 feeder/50-ha.

Capture

Over the course of eight years, we captured 116 adult deer ($\geq$ 1 year old) on the 2,550-ha portion of Brosnan Forest located north of Highway 78. We collared 42 males during 2009–2011, 43 females during 2013–2015, and 31 deer (15 males and 16 females) during 2017–2018. We sedated all deer with an intramuscular injection of a pre-mixed dose of xylazine (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml given at a rate of 2.2 mg/kg) and Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa; 100 mg/ml given at a rate of 4.5 mg/kg) using a 2 cc Type C Pneu-Dart fired by a Pneu-Dart Model 389 tranquilizer gun (Pneu-dart Inc., Williamsport, Pennsylvania). We estimated the age of all deer using tooth replacement and wear characteristics (Severinghaus 1949). We attached GPS collars (Model G2110D; Advanced Telemetry Systems, Isanti, Minnesota) weighing approximately 410 grams to the neck of each deer, and affixed the collars so they would remain in an upright position to ensure that they acquired accurate fixes (D'Eon and Delaparte 2005) and were loose enough to allow for growth and prevent restriction. To allow for additional growth and neck swelling during the breeding season, we lined the collars fitted to males with a pliable foam material. Once we completed collaring and handling, and at least 30 min had elapsed from the time we darted the deer, we injected each deer with a 3-ml intramuscular dose of Tolazoline (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml given at a rate of 6.6 mg/kg) to act as a reversal to the xylazine. Following the injection of the reversal, we monitored the deer from a distance until they moved away under their own power. These protocols were approved by the Auburn University Animal Care and Use Committee (PRN#2008-1489, PRN#2013-2205, PRN#2017-2996).

GPS Data Collection

The time of year during which radio collars collected data varied among years of the study, lasting from 24 August through 23 November in 2009-2011, 16 August through 15 December in 2013-2015, and 1 August through 15 January of the following year in 2017 and 2018. Since collared deer on Brosnan Forest were vulnerable to hunter harvest, and some collars malfunctioned prior to completing the collection period, the length of the collection period also varied among deer within the same year. We programed all collars to acquire GPS locations at a rate of one attempted fix every 30 min. Along with each GPS location recorded in UTM coordinates, the collars recorded date, time, altitude, fix status, satellites, position dilution of precision (PDOP), horizontal dilution of precision (HDOP), temperature, and activity sensor data. We programed the collars to automatically release from the deer following the data collection period. Following collar release, or mortality we located the collars using VHF radio telemetry after they had been released.

GPS Data Management

We removed three-dimensional GPS locations with a PDOP > 10 or an HDOP > 6 along with any 2-dimensional fixes with an HDOP > 3 (D'Eon and Delparte 2005; Lewis et al. 2007). In addition, we imported the data into ArcMap 10.4.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA) where we visualized and removed inaccurate fixes. All deer were collared ≥18 days prior to the start of the collection period, therefore we assumed that the collection period did not include any capture-related behavioral changes.

We created a two-state hidden Markov model using the *R* package momentuHMM to classify each GPS location as either 'active' or 'inactive' following the example presented by McClintock and Michelot (2018). The model utilized step length and turning angle to classify

each location into one of two behavioral states. Short step lengths and tighter turning angles characterized the inactive state, while longer step lengths and straighter paths characterized the active state. Additionally, we applied a maximum threshold distance between successive GPS locations that could be classified as inactive. To overcome potential biases associated with using thresholds from collars with differing accuracy, we used a conservative metric of four times the average error as a maximum threshold value between successive points for classifying GPS locations as inactive (Jerde and Visscher 2005, Sullivan et al. 2016). We considered all Euclidean distances between points greater than or equal to four times the average error distance as active. Accuracy tests revealed that collars deployed in the last two years of the study were substantially more accurate than those used in previous years, therefore we used threshold values of 51.78 m for 2009-2015 and 29.08 m for the 2017-2019 data. We derived these maximum distance thresholds from collar accuracy tests. To conduct these tests, we positioned test collars 1m above the ground (the approximate height of the neck of a white-tailed deer) with the antenna pointing vertically upward, and left them to collect GPS locations for approximately five days in different cover types found throughout the study area. We then compared the positional accuracy relative to the location of the collar as determined by a Trimble Geo 7X GPS (accurate to $\leq$ 1 m). To reduce bias, we restricted activity classification to GPS locations collected at the scheduled 30-min intervals, and we excluded points from analyses when the inter-fix interval was longer than 30 min between successive locations.

Wind Speed and Brightness Index

We obtained weather condition and wind speed data, collected at 20-min intervals at the monitoring station at Summerville Airport, Summerville, South Carolina (21.6 km southeast of the study area) via http://mesowest.utah.edu. We used the suncalc package in program *R* to

obtain the fraction of the moon illuminated and the altitude (in radians) of the moon above the horizon for each GPS location, we then converted the altitude to range on a scale from 0 (even with horizon) to 1 (highest point in the sky). Additionally, we obtained sunrise, sunset, moonrise, and moonset for each day at Brosnan Forest (33°09'18.1"N, 80°25'44.5"W). We defined night as the period lasting from 30 min after sunset to 30 min before sunrise, and modified the moonlight risk index (MRI) used by Gigliotti and Diefenbach (2018) to create the nighttime brightness index. The brightness index ranged from 0 to 1, and was a function of the fraction of the moon illuminated, multiplied by the altitude of the moon above the horizon. If the moon was not above the horizon, the brightness value was set to 0. To account for light reduction due to cloud cover, we used categorical weather condition variables. If the weather condition was clear, we multiplied the brightness value by 1, if it was partly cloudy or broken clouds we multiplied the brightness value by 0.5, and if it was overcast or any other condition that would greatly reduce nighttime brightness (e.g., fog, rain, snow) we multiplied brightness by 0. Additionally, due to the variation in start and end dates of data collection among years, and the tendency for deer activity to vary throughout the seasons encompassed by our sampling period (Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010, Masse and Côté 2013), we created a numeric sampling date variable that started August 1st each year.

Data Analysis

Due to differing constraints related to body size and behavioral differences among sexes (Webb et al. 2010) we modeled males and females separately. We used a generalized additive logistic modeling (GAM) approach, due to the flexibility of GAMs to incorporate non-linear smoothing, and a binary response variable. Since we expected sampling date to affect activity

throughout the sampling period in a non-linear fashion, we included a smoothing term of

sampling date in all models. Additionally, to account for potential differences among individual

deer, we applied a random smoothing effect of individual in all models. For each sex, we

considered five competing models, a biologically informed null model that included a smoothing

variable for sampling date and random effect of individual, and four models with additional

variables included as linear predictors. We compared all models using AIC_c (Burnham and

Anderson 2002) and conducted all analyses in program R (v3.5.2; R Core Development Team

2018).

Results

Of the 116 deer captured over the course of this study, 9 were removed from analysis due

to collar malfunction or death prior to the sampling period. We classified activity for nighttime

GPS locations from the remaining 54 males ($n = 95{,}785$ locations) and 53 females ($n = 122{,}021$

locations). The highest ranking models for both male (Table 1.1) and female (Table 1.2)

probability of activity had interacting effects of brightness index and wind speed.

Probability of male activity varied little with fluctuating brightness and wind speed

(Figures 1.1 and 1.2). We estimated that for each 0.10 increase in brightness index, males were

1.02 (1.01-1.03; 95% C. L.) times as likely to be active ($P < 0.01$). We estimated that for each 5

km/hr increase in wind speed, males were 1.03 (1.01-1.04; 95% C. L.) times as likely to be

active ($P < 0.01$). During darker periods, estimated probability of male activity was relatively

stable, increasing slightly with increasing wind speed (Figure 1.3). When brightness index

values were moderate, probability of male activity was stable. During the brighter periods, the

probability of male activity decreased slightly with increasing wind speed.

For each 0.10 increase in brightness index, females were 1.01 (1.01-1.02; 95% C. L.)

times as likely to be active ($P < 0.01$). Accordingly, estimated probability of female activity was

0.65 (SE = 0.016), 0.68 (SE = 0.018), and 0.70 (SE = 0.026) at brightness index values of 0, 0.5, and 1 respectively (Figure 1.4). Additionally, female activity decreased with increasing wind speed, and females were 0.92 (0.90-0.93; 95% C.I.) times as likely to be active with each 5 km/hr increase in wind speed. Estimated probability of female activity was 0.67 (SE = 0.016), 0.63 (SE = 0.024), and 0.58 (SE = 0.041) at 0, 15, and 30 km/hr respectively (Figure 1.5). During darker periods, the estimated probability of female activity decreased with increasing wind speed, and when the brightness index value was 0, estimated probability of activity was 0.66 (SE = 0.017), 0.60 (SE = 0.023), and 0.54 (SE = 0.040) at 0, 15, and 30 km/hr respectively (Figure 1.6). At moderate levels of brightness, probability of female activity did not change with respect to wind speed. At greater brightness index values, increasing wind speed had a positive effect on estimated probability of activity, and was 0.69 (SE = 0.027), 0.74 (SE = 0.081), and 0.79 (SE = 0.167) at 0, 15, and 30 km/hr respectively when the brightness index was 1.0 (Figure 1.6).

Discussion

Our data suggest that increasing nighttime brightness had a positive effect on deer activity during our study. While probability of female activity was associated positively with brightness, probability of male activity, although significant, tended to be only marginally greater during nights that were brighter. Other studies have reported similar relationships between nighttime brightness and deer activity. Buss and Harbert (1950) observed more mule deer at salt licks on full moon nights, Colino-Rabanal et al. (2018) found that more deer-vehicle collisions occurred on full moon nights, and Kammermeyer (1975) found that deer were more active during brighter phases of the moon. However, our results differ from most other investigations (Zagata and Haugen 1974, Kufeld 1988, Beier and McCollough 1990, and Webb

et al. 2010), which may be due to differences in sampling methods. Zagata and Haugen (1974) used direct observations which required the observer to be physically present, and may have altered natural behaviors and activity patterns of deer (Bridges and Noss 2011). Webb et al. (2010) found no differences among moon phases using fine-scale GPS data, however, we were interested in understanding the influence of nighttime brightness, which can be influenced by moon phase, but is also influenced by the position of the moon in the sky and weather variables. Beier and McCullough (1990) conducted the most comprehensive investigation into lunar variables relative to activity, analyzing the effect of moon phase, moon presence, and moon visibility (the product of moon presence and the percentage of sky free of opaque cloud cover), but found no effect of these variables. Since we saw differences between males and females, combining sexes may have limited the inferential ability of Beier and McCullough (1990). Additionally, since they combined their data into 3-hour blocks of activity, and brightness variables can change rapidly, they may have had a reduced ability to detect differences at short time scales.

The positive relationship we observed between nighttime brightness and probability of deer activity differs from the bulk of the published data, most of which relates to small mammals (Prugh and Golden 2014). Most studies have reported that small mammals are more active during darker conditions (Beier 2006). Responses to light and darkness in mammals depends largely on optical anatomy and physiology, which differ between small mammals and deer (Beier 2006). For example, small skull size in small mammals limits the number of rods their eyes can possess, thereby limiting visual resolution (Beier 2006). Additionally, the tapetum lucidum is present in the eyes of deer, and improves vision in low-light conditions (D'Angelo et al. 2008), but is lacking in many small mammal species (Beier 2006). Improved vision under

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brighter nighttime conditions may enhance the ability of deer to detect predators (Birgersson et al. 2001, VerCauteren and Pipas 2003), making brighter nights less risky. There is some evidence to support increased pack hunting by coyotes during darker moon phases (Bender et al. 1996) which may be advantageous for hunting larger prey such as adult deer (Benson and Patterson 2013, Muntz and Patterson 2004, but see Patterson and Messier 2000). Accordingly, sight may play a role in deer foraging (Birgersson et al. 2001), and brighter nighttime conditions may allow deer to forage more effectively given that deer vision is particularly well suited for crepuscular periods (Cohen et al. 2014). Conversely, due to anatomical constraints, small mammalian sight lacks the resolution capabilities of deer, and other senses (i.e., olfaction) are more important for foraging (Beier 2006). Therefore, small mammalian foraging efficiency may be impacted less by light, while other factors such as increased risk of predation (Clarke 1983) drive decreases in small mammal activity on brighter nights. The predation risk allocation hypothesis predicts that animals can perceive risk and adjust behavior accordingly (Lima and Bednekoff 1999). The decrease in activity we saw for females on darker nights may therefore be due to a combination of decreased foraging efficiency and increased risk of predation to them and their offspring.

The influence of wind speed on probability of activity differed between males and females. Greater wind speed can alter the ability of deer to detect predators (Cherry and Barton 2017). Additionally, sexual dimorphism in ungulate body size may lead to differences in predation rates between sexes (Bleich and Taylor 1998, Pierce et al. 2000, but see Sinclair et al. 2003). Therefore, the differences we observed in the relationship between wind speed and activity of males and females may be due to greater perceived risk of predation for females. Investigators have reported predation on females more often than for male deer in the

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southeastern United States (Labisky and Boulay 1998, Kilgo et al. 2016). Additionally, females often travel in family groups that contain fawns (Hawkins and Klimstra 1970), and fawns are regularly predated in the southeastern United States (Kilgo et al 2010, Kilgo et al. 2012, McCoy et al. 2013, Nelson et al. 2015). Activity of females may therefore be reflective of predation risk for more vulnerable individuals within the group (i.e., fawns), as has been reported with vigilance behavior (Olson et al. 2019). Our data agree with some investigations into deer activity/movement relative to wind speed, but conflict with the findings of others. For example, Webb et al. (2010) observed a decrease in movement rate as wind speed increased, and likewise, Montague et al. (2017) detected fewer deer during thermal imaging surveys with increasing wind speed. In contrast with these studies, Zagata and Haugen (1974) observed more deer as wind speed increased, and others found no effect of wind speed on deer activity in general (Kammermeyer 1975, Kufeld et al. 1988), or at night specifically (Webb et al. 2010). Conflicting results among these studies may be due to differences in sampling methods (i.e., direct observation, activity sensors, and telemetry). Direct observation can be confounded by wind-influenced differences in detection ability. For example, deer may avoid human observers due to scent carried by the wind, which can be affected by wind speeds (Brady et al. 1995, Cablk et al. 2008, Ruzicka and Conover 2012, Munoz et al. 2014, Togunov et al. 2016), or shift to using cover types that influence observability (Ozoga and Gysel 1972, Beier and McCullough 1990). Investigations using animal-borne activity sensors and tracking devices limit the aforementioned confounding factors, but have often been limited by small sample (i.e., < 30 deer) and the need to group data for analysis. Additionally, investigations into deer behavior relative to wind speed have been conducted in different areas of the white-tailed deer's range.

Regional vegetation, terrain, and climatic variables differ among these studies, likely influencing local winds and deer activity in the presence of various wind speeds.

Independently, brightness (Wells 1978, Prugh and Golden 2014) and wind speed (Ruzicka and Conover 2011, Cherry and Barton 2017) have been found to influence sensory abilities and activity in both predator and prey species. However, our data indicate there is an interactive effect of wind speed and brightness on nighttime activity of female deer. Under dark conditions, female deer tended to be less active as wind speed increased. Darker nighttime periods, combined with greater winds speed hinder the three primary senses (i.e., vision, olfaction, and hearing) used by deer to detect predators (Sauer 1984, D'Angelo et al. 2008, Ditchkoff 2011). This decrease in sensory ability can increase perceived risk of predation and cause female deer to reduce the amount of time they are active (Lima and Bednekoff 1999). Alternatively, fewer senses are impaired when it is dark and less windy or bright and windy. We observed that at moderate brightness levels, wind speed did not affect activity, and under the brightest conditions probability of activity increased with increasing wind speed. Although we observed substantial variation with differing values of nighttime brightness and wind speed, overall probability of nighttime activity is still relatively high, and is greater than during daytime activity rates reported elsewhere (Massé and Côté, 2013, Sullivan et al. 2016, Wiskirchen 2017). This may indicate that even with potential predation risk associated with abiotic factors at night, endogenous rhythms still have a stronger influence on activity.

Literature Cited

Allen, T., R. Southwick, and D. Howlett. 2013. Hunting in America: an economic force for conservation. National shooting sports foundation and Association of fish and wildlife agencies.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs 109:3-51.

Beier, P. 2006. Effects of artificial lighting on terrestrial mammals. Pages 19-42 in T. Longcore, and C. Rich, editors. Ecological consequences of artificial night lighting. Island Press, Washington, D. C., USA.

Bender, D. J., E. M. Bayne, and R. M. Brigham. 1996. Lunar condition influences coyote (*Canis latrans*) howling. The American Midland Naturalist 136:413-417.

Benson, J. F., and B. R. Patterson. 2013. Moose (*Alces alces*) predation by eastern coyotes (*Canis latrans*) and eastern coyote x eastern wolf (*Canis latrans* x *Canis lycaon*) hybrids. Canadian Journal of Zoology 91:837-841.

Birgersson, B., U. Alm, and B. Forkman. 2000. Colour vision in fallow deer: a behavioural study. Animal Behaviour 61:367-371.

Bleich V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265-272.

Bonnot, N. C., N. Morellet, A. J. M. Hewison, J-L. Martin, S. Benhamou, and S. Chaamaillé-Jammes. 2016. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm to the absence of predators. Canadian Journal of Zoology 94:385-394.

Bowers, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. Journal of Mammalogy 69:201-204.

Brady, J., N. Griffiths, and Q. Paynter. 1995. Wind speed effects on odour source location by

    tsetse flies (*Glossina*). Physiological Entomology 20:293-302.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a

    practical information-theoretic approach. Second edition. Springer, New York, New

    York, USA.

Cablk, M. E., J. C. Sagebiel, J. S. Heaton, and C. Valentin. 2008. Olfaction-based detection

    distance: a quantitative analysis of how far away dogs recognize tortoise odor and follow

    it to source. Sensors 8:2208-2222.

Cherry, M. J., L. M. Conner, and R. J. Warren. 2015. Effects of predation risk and group

    dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral

    Ecology 26: 1091-1099.

Cherry, M. J., and B. T. Barton. 2017. Effects of wind on predator-prey interactions. Food Webs

    13:92-97.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2014. Confirmation of

    coyote predation on adult female white-tailed deer in the southeastern United States.

    Southeastern Naturalist 13:30-32.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls

    (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behavioral ecology and

    Sociobiology 13:205-209.

Colino-Rabanal, V. J., T. A. Langen, S. J. Peris, and M. Lizana. 2018. Ungulate: vehicle

    collision rates are associated with the phase of the moon. Biodiversity and Conservation

    27:681-694.

Collier, B. A., S. S. Ditchkoff, J. B. Raglin, and J. M. Smith. 2007. Detection probability and

sources of variation in white-tailed deer spotlight surveys. Journal of Wildlife Management 71:277-281.

Collins, C., and R. Kays. 2011. Causes of mortality of North American populations of large and medium-sized mammals. Animal Conservation 14:474-483.

Cooper Jr., W.E., and D. T. Blumstein, editors. 2015. Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge UK.

D'Angelo, G. J., A. Glasser, M. Wendt, G. A. Williams, D. A. Osborn, G. R. Gallagher, R. J. Warren, K. V. Miller, and M. T. Pardue. 2008. Visual specialization of an herbivore prey species, the white-tailed deer. Canadian Journal of Zoology 86:735-743.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383-388.

Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed deer support mate-competition theory. Journal of Wildlife Management 65:552-559.

Ditchkoff, S. S. 2011. Anatomy and physiology. Pages 43-73 in D. G. Hewitt (ed.). Biology and management of white-tailed deer. Taylor and Francis Group, Boca Raton, FL.

Doucet, J. G., and J. R. Bider. 1974. The effects of weather on the activity of the masked shrew. Journal of Mammalogy 55:348-363.

Gigliotti, L. C., and D. R. Diefenbach. 2018. Risky behavior and its effect on survival: snowshoe hare behavior under varying moonlight conditions. Journal of Zoology 305:27-34.

Gilbert, B. S., and S. Boutin. 1991. Effect of moonlight on winter activity of snowshoe hares. Arctic and Alpine Research 23:61-65.

Gulsby, W. D., M. J. Cherry, J. T. Johnson, L. M. Conner, and K. V. Miller. 2018. Behavioral response of white-tailed deer to coyote predation risk. Ecosphere 9(3):e02141.10.1002/ecs2.2141.

Hawkins, R. E., and W. D. Klimstra. 1970. A preliminary study of the social organization of the white-tailed deer. Journal of Wildlife Management 34:460-464.

Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377-387.

Heffelfinger, J. R. 2011. Taxonomy, Evolutionary History, and Distribution. Pages 3-39 in D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Hewitt D. G. 2011. Nutrition. Pages 75-106 in D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parameterization. Ecological Applications 15:806-810.

Julien-Laferriere, D. 1997. The influence of moonlight on activity of woolly opossums (*Caluromys philander*). Journal of Mammalogy 78:251-255.

Kammermeyer, K. E. 1975. Movement-ecology of white-tailed deer in relation to a refuge and hunted area. Thesis, University of Georgia, Athens, Athens, Georgia, USA.

Kammermeyer, K. E., and R. L. Marchinton. 1977. Seasonal change in circadian activity of radio-monitored deer. Journal of Wildlife Management 41:315-317.

Kilgo, J. C., H. S. Ray, C. R. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in Southeastern North America? Journal of Wildlife Management 74:929-933.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420-1430.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747-753.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. McNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638-652.

Kramer, K. M., and E. C. Birney. Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. Journal of Mammalogy 82:535-544.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1988. Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. Journal of Range Management 41:515-522.

Labisky, R. F., and M. C. Boulay. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. The American Midland Naturalist 139:275-281.

Lauerman, S. 2007. Effects of season of fire on red cockaded woodpecker (*Picoides borealis*) reproduction and the breeding bird community of a longleaf pine ecosystem. Thesis, Clemson University, Clemson, South Carolina USA.

Lawler, S. P. 1989. Behavioral responses to predators and predation risk in four species of larval anurans. Animal Behaviour 38:1039-1047.

Leuthold, W. 1977. African ungulates: a comparative review of their ethology and behavioral

    ecology. Springer-Verlag, New York, New York.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS

    collar performance: using data screening to reduce location error. Journal of Applied

    Ecology 44:663–671.

Little, A. R., S. Demarais, K. L. Gee, S. L. Webb, S. K. Riffell, J. A. Gaskamp, and J. L. Belant.

    2014. Does human predation risk affect harvest susceptibility of white-tailed deer during

    hunting season? Wildlife Society Bulletin 38:797-805.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator

    behavior: the predation risk allocation hypothesis. The American Naturalist 153:649-659.

Lingle, S., and W. F. Wilson. 2001. Detection and avoidance of predators in white-tailed deer

    (*Odocoileus virginianus*) and mule deer (*O. hemionus*). Ethology 107:125-147.

Loe, L. E., C. Bonenfant, A. Mysterud, T. Severinsen, N. Oritsland, R. Langvatn, A. Stien, R. J.

    Irvine, and N. C. Stenseth. 2007. Activity pattern of arctic reindeer in a predator-free

    environment: no need to keep a daily rhythm. Population Ecology 152:617-624.

Massé, A., and S. D. Coté. 2013. Spatiotemporal variations in resources affect activity and

    movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density.

    Canadian Journal of Zoology 91:252-263.

McClintock, B. T., and T. Michelot. 2018. momentuHMM: R package for generalized hidden

    Markov models of animal movement. Methods in Ecology and Evolution 9:1518-1530.

McCoy, J. C., S. S. Ditchkoff, J. B. Raglin, B. A. Collier, and C. Ruth. 2013. Factors influencing

    survival of white-tailed deer fawns in coastal South Carolina. Journal of Fish and

    Wildlife Management 4:280-289.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. Linking anti-predator behavior to prey demography reveals limited risk of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Montague, D. M., R. D. Montague, M. L. Fies, and M. J. Kelly. 2017. Using distance-sampling to estimate density of white-tailed deer in forested, mountainous landscapes in Virginia. Northeastern Naturalist 24:505-519.

Muñoz, D., J. Kapfer, and C. Olfenbuttel. 2014. Do available products to mask human scent influence camera trap survey results? Wildlife Biology 20:246-252.

Muntz, E. M., and B. R. Paterson. 2004. Evidence for the use of vocalization to coordinate the killing of a white-tailed deer, *Odocoileus virginianus*, by coyotes, *Canis latrans* The Canadian Field-Naturalist 118:278-280.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. PNAS 105: 19052-19059.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. M. Conner. 2015. Coyote and bobcat predation on white-tailed deer fawns in a longleaf pine ecosystem in southwestern Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:208-213.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not direct, cues of predation risk. Behavioral Ecology 15:433-437.

Owen-Smith, N., and L. W. Traill. 2017. Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food? Journal of Zoology 4:281-290.

Ozoga, J. J, and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. Journal of Wildlife Management 36:892-896.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Pratas-Santiago, L. P., A. L. S Goncalves, A. J. A. Nogueira, and W. R. Spironello. 2017. Dodging the moon: the moon effect on activity allocation of prey in the presence of predators. Ethology 123:467-474.

Ruzicka, R. E., and M. R. Conover. 2012. Does weather or site characteristics influence the ability of scavengers to locate food? Ethology 118:187-196.

Saalfeld, S. T., and S. S. Ditchkoff. 2007. Survival of neonatal white-tailed deer in and exurban population. Journal of Wildlife Management 71:940-944.

Sabato, M. A. L., L. F. B. de Melo, E. M. V. Magni, R. J. Young, and C. M. Coelho. 2006. A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. Behavioral Processes 73:228–230.

Sauer, P. R. 1984. Physical characteristics. Pages 73-90 in L. K. Howells, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-215.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288-290.

Stander, P. E. 1992. Foraging dynamics of lions in a semi-arid environment. Canadian Journal of Zoology 70:8-21.

Stander, P. E., and S. D. Albon. 1993. Hunting success of lions in a semi-arid environment. Symposia of the Zoological Society of London 65:127-143.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159-2173.

Stitch, H-B., and Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293:396-398.

Sullivan, J. D., S. S. Ditchkoff, B. A. Collier, C. R. Ruth, and J. B. Raglin. 2016. Movement with the moon: white-tailed deer activity and solunar events. Journal of the Southeastern Association of Fish and Wildlife Agencies 3:225-232.

Sullivan, J. D., S. S. Ditchkoff, B. A. Collier, C. R. Ruth, and J. B. Raglin. 2018. Recolonizing the danger zone: response of female white-tailed deer to discrete hunting events. Wildlife Biology DOI: 10.2981/wlb.00455.

Togunov, R. R., A. E. Derocher, and N. J. Lunn. 2017. Windscapes and olfactory foraging in a large carnivore. Scientific Reports 7:46332.

U.S. Department of the Interior, U.S. Fish and Wildlife Service, U.S. Department of Commerce, and U.S. Census Bureau. 2014. 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.

Valix, M., H. Fritz, A. J. Loveridge, Z. Davidson, J. E. Hill, F. Murindagomo, and D. W. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behavior at waterholes? Behavioral Ecology and Sociobiology 63:1483-1494.

VerCauteren, K. C., and M. J. Pipas. 2003. A review of color vision in white-tailed deer. Wildlife Society Bulletin 31:684-691.

Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. DeYoung. 2010. Measuring

fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology 2010:1-12.

Wells, M.C. 1978. Coyote senses in predation: environmental influences on their relative use. Behavioural Processes 3:149-158.

Wells, M. C., and P. N., Lehner. 1978. The relative importance of the distance senses in coyote predatory behavior. Animal Behaviour 26:251-258.

White, S. W., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225-237.

Wiskirchen, K. H. 2017. Survival of adult white-tailed deer and movement relative to temporal patterns of predation risk. Thesis, Auburn University, Auburn, Alabama, USA.

Table 1.1. Candidate models, degrees of freedom (df), Akaike's Information Criterion (AIC$_c$), and associated model ranks (ΔAIC$_c$) and model weights (w_i) used to predict the effect of nighttime brightness and wind speed on probability of activity of adult male white-tailed deer at Brosnan Forest, South Carolina.

Model	df	AIC$_c$	ΔAIC$_c$	w_i
s(Sampling Date)+Brightness*Wind Speed	12	110876.2	0.00	0.97
s(Sampling Date)+Brightness+Wind Speed	11	110883.3	7.10	0.03
s(Sampling Date)+Brightness	10	110886.5	10.28	0.01
s(Sampling Date)+Wind Speed	10	110908.1	31.82	0.00
s(Sampling Date)	9	110909.0	32.79	0.00

Table 1.2. Candidate models, degrees of freedom (df), Akaike's Information Criterion (AIC$_c$), and associated model ranks (ΔAIC$_c$) and model weights (w_i) used to predict the effect of nighttime brightness and wind speed on probability of activity of adult female white-tailed deer at Brosnan Forest, South Carolina.

Model	df	AIC$_c$	ΔAIC$_c$	w_i
s(Sampling Date)+Brightness*Wind Speed	12	163825.9	0.00	1.00
s(Sampling Date)+Brightness+Wind Speed	11	163855.5	29.58	0.00
s(Sampling Date)+Wind Speed	10	163927.3	101.40	0.00
s(Sampling Date)+Brightness	10	163987.8	161.92	0.00
s(Sampling Date)	9	164093.5	267.59	0.00
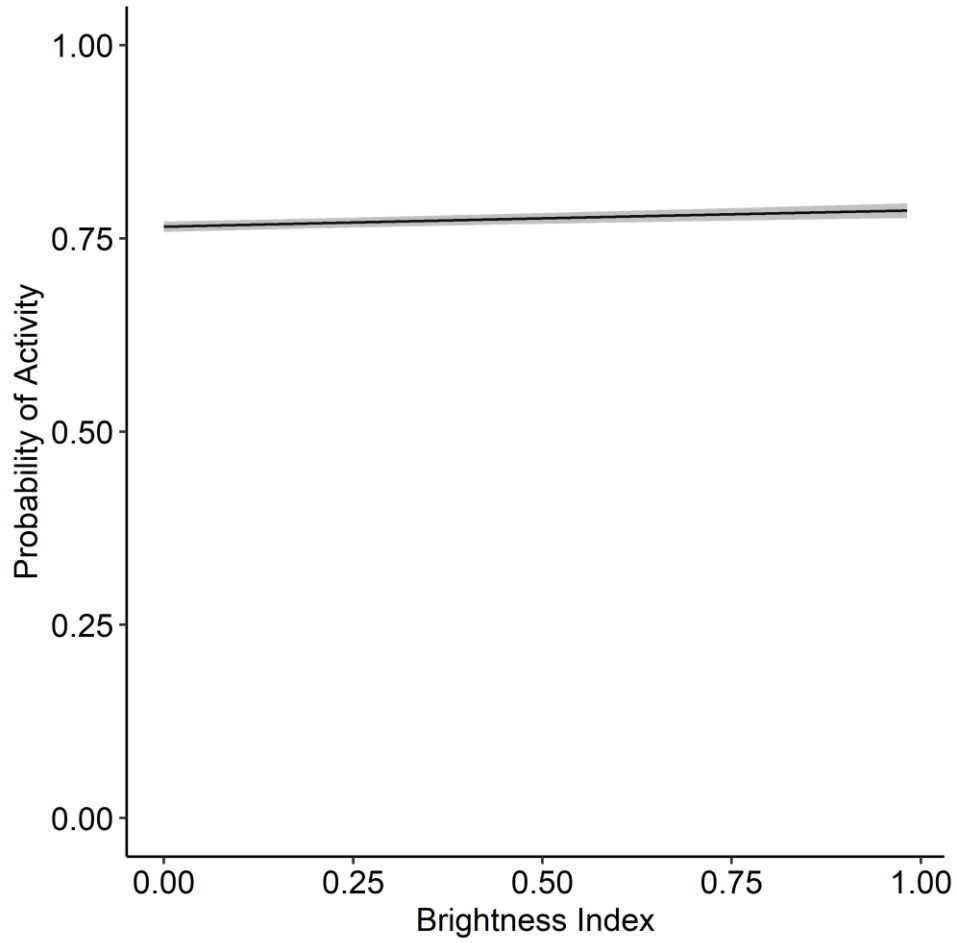
Figure 1.1. Model estimated probability of activity relative to Brightness Index for male white-tailed deer at Brosnan Forest, South Carolina.
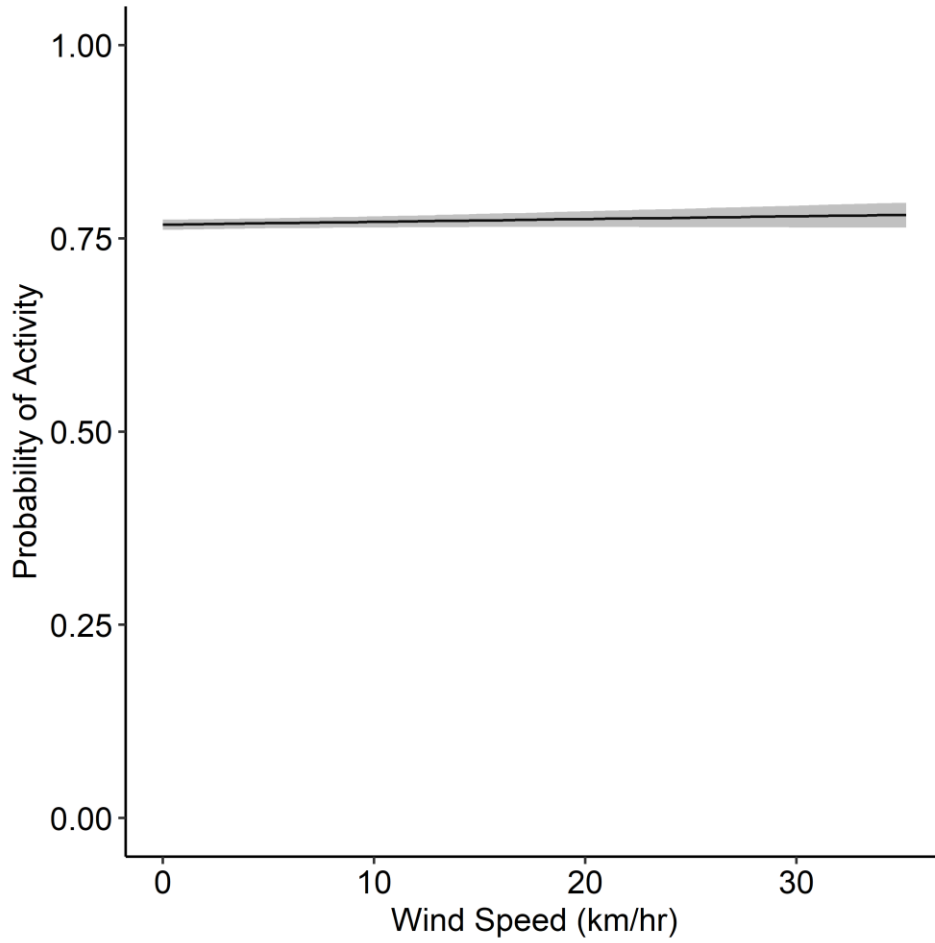
Figure 1.2. Model estimated probability of activity relative to wind speed (km/hr) for male white-tailed deer at Brosnan Forest, South Carolina.
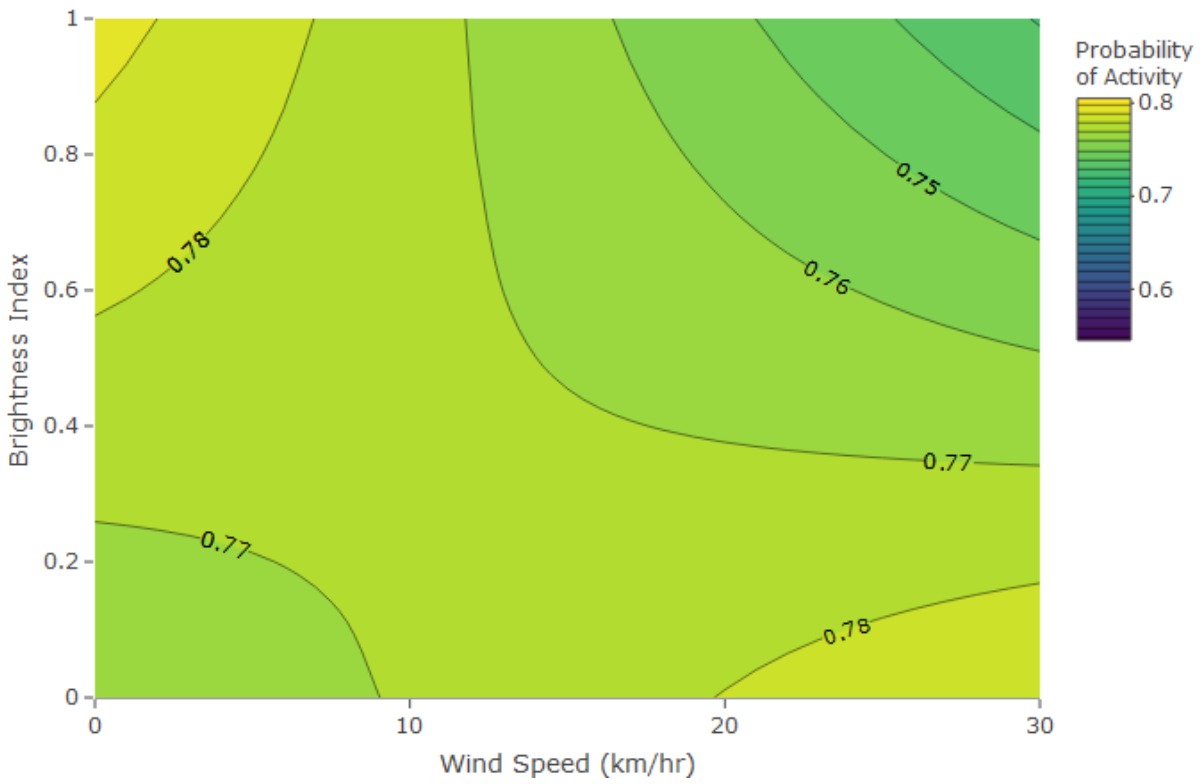
Figure 1.3. Model estimated probability of activity relative to wind speed (km/hr) and brightness index for male white-tailed deer at Brosnan Forest, South Carolina.
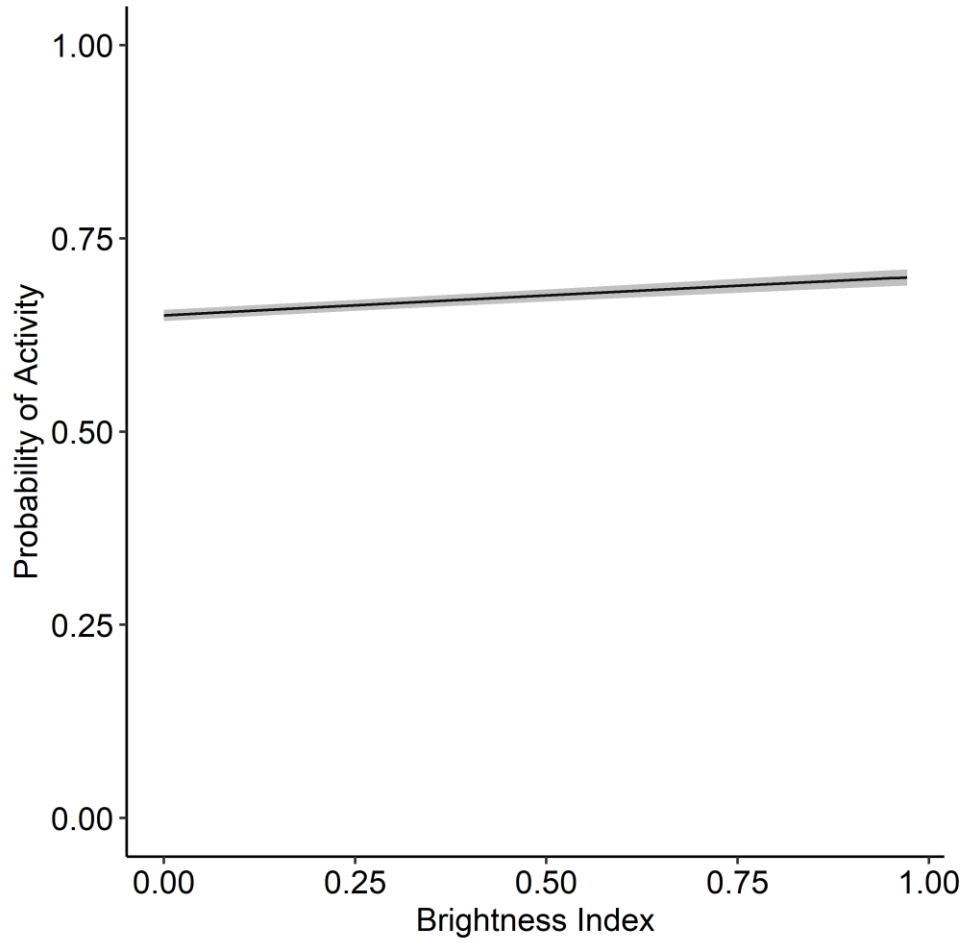
Figure 1.4. Model estimated probability of activity relative to Brightness Index for female white-tailed deer at Brosnan Forest, South Carolina.
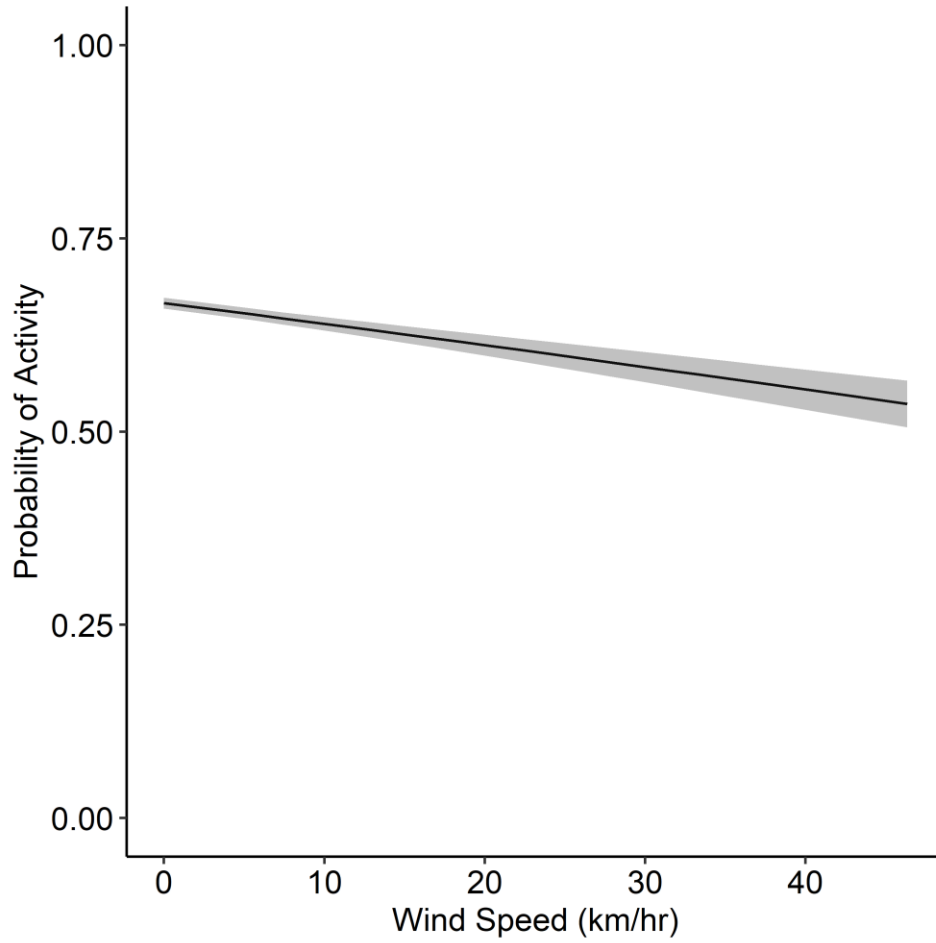
Figure 1.5. Model estimated probability of activity relative to wind speed (km/hr) for female white-tailed deer at Brosnan Forest, South Carolina.
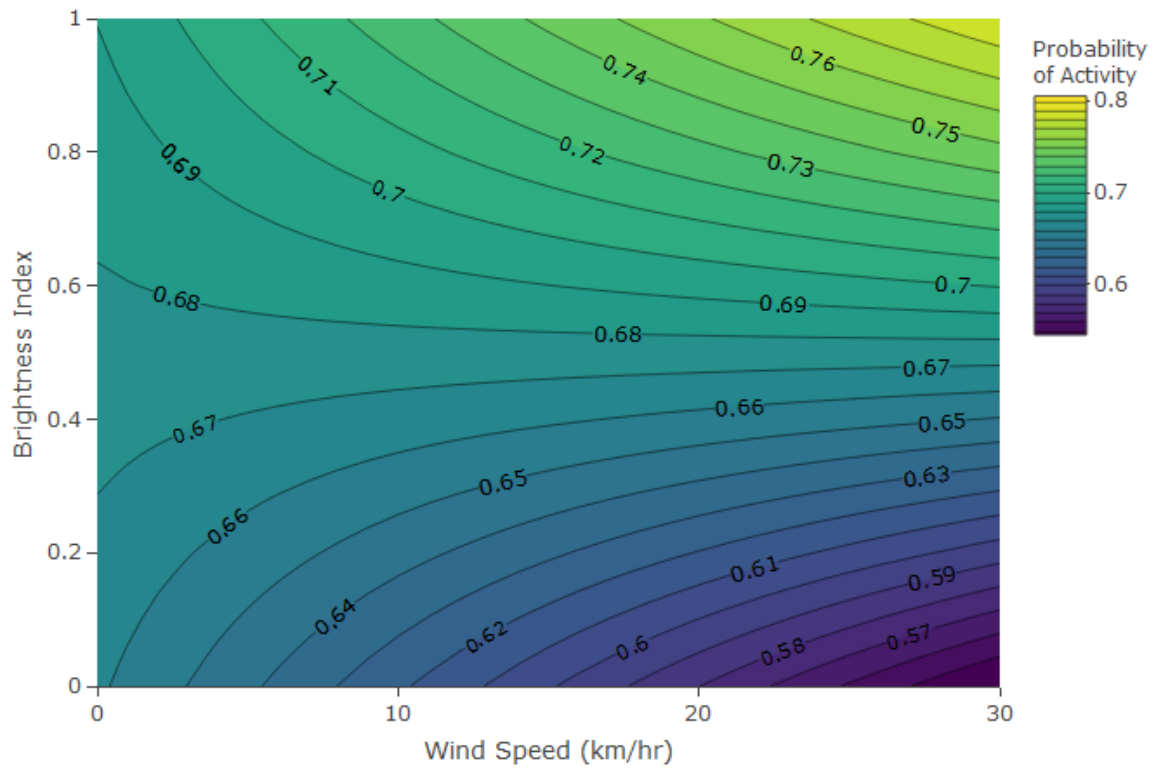
Figure 1.6. Model estimated probability of activity relative to wind speed (km/hr) and brightness index for female white-tailed deer at Brosnan Forest, South Carolina.

Chapter 2: Effect of abiotic factors on activity of white-tailed deer (*Odocoileus virginianus*)
in South Carolina

Abstract

Internal and external factors influence behavior of all animals, and in order to successfully survive and reproduce, animals must be adapted to live with the complex array of biotic and abiotic factors present in their environment. Dynamic abiotic factors (e.g., wind, temperature, and moon phase) are continuously present and constantly changing in the environment of all animals, and actions animals take in response to these abiotic factors have the potential to affect survival and lifetime fitness. Measuring behavioral responses to abiotic factors is an important step in understanding interactions between animals and the environment in which they live. To investigate how white-tailed deer (*Odocoileus virginianus*) in the Southeast interact with their environment, we captured and GPS-collared 116 adult white-tailed deer from 2009-2018 in South Carolina, USA. We classified each GPS location as active or inactive based on interfix step length, turning angles, and collar accuracy information. Additionally, we acquired abiotic factor data from a long-term monitoring station located near the study site. We modeled the effect of each abiotic factor on activity separately using logistic regression. We observed that weather condition, temperature, wind speed, barometric pressure, moon phase, and moon position affected activity in some seasons and times of day. Activity responses suggest that deer in the Southeast may be adjusting activity to decrease thermal stress and increase foraging efficiency and predator detection. However, responses to abiotic factors were typically less pronounced than circadian fluctuations in activity, and occurred most often during non-peak times of activity.

Introduction

The ecosystem in which an animal lives consists of a complex and constantly changing array of biotic and abiotic factors. Animals that are well adapted to these factors are generally considered the most ecologically fit, and are subsequently more likely to survive and successfully reproduce. These factors continually exert their influence on animals through both direct and indirect pathways. For example, water is an abiotic factor that is fundamentally important for life, and the inability to acquire water can lead to death; consequently, many African large mammal species congregate closer to water holes during the dry season (Ayeni 1975). However, the risk of encountering lions (*Panthera leo*) generally increases near water sources (Valix et al. 2009), hence there is a potential cost as well. The need to balance biological requirements and risk of predation is often mediated by behavioral adjustments. Accordingly, Valix et al. (2009) observed that large mammalian prey species adjusted behaviorally to increased risk around water holes by increasing vigilance and shifting their use of water holes to times when they were less likely to encounter lions. Other abiotic factors are not as integral to life, but their influence shapes interactions between animals and their environment and interactions among predator and prey species. For example, greater wind speeds can directly influence the thermoregulatory ability of sage grouse (*Centrocercus urophasianus*) during colder conditions (Sherfy and Pekins 1995), and indirectly influence fitness by increasing the success rates of nest predators (Ruzicka and Conover 2012, Webb et al. 2012).

Dynamic abiotic factors like wind speed, temperature, and other weather and climatic variables, are often rapidly changing or cyclical, and can affect both animal biology and behavior. Accordingly, animals have adapted a suite of biological responses to reduce the negative effects of stress associated with abiotic factors. For example, the thermal properties of

white-tailed deer (*Odocoileus virginianus*) pelage vary by region to maximize insulation on parts of the body that are most exposed to the weather, and seasonally to maximize insulation during colder times of the year (Jacobsen 1980). Obvious physiological responses (i.e., morphological adaptations) have been extensively studied and are generally well understood. More nuanced behavioral responses to abiotic factors can also be advantageous. For example, de Lamo et al. (1998) found that guanacos (*Lama guanicoe*) during cold, windy conditions bed with their hindquarters, an area with longer fur, facing toward the wind. Behavioral responses such as these are employed by all species to offset stresses and negative impacts induced by the spectrum of abiotic factors.

White-tailed deer have successfully adapted to live in a vast area that extends from the Canadian Yukon south to Peru and Bolivia. Accordingly, there are massive differences in climate, vegetative communities used for forage and cover, anthropogenic landscape modification, and predator communities across this range. However, white-tailed deer have been able to successfully exploit these different environments, and are abundant throughout much of their range (DeYoung 2011). Their success across this diversity of landscapes and environmental conditions is due to their ability to adapt to a variety of conditions, and physical and physiological differences (e.g., body size, fur thickness, and fat storage) among the different subspecies of white-tailed deer has been at the foundation of their success (Ditchkoff 2011, Johns et al. 1984). White-tailed deer have also developed a variety of behavioral adaptations across their range. For example, white-tailed deer in northern populations migrate to yarding areas (Ozoga and Gysel 1972) during winter to reduce thermal stress, while deer in other regions do not. Alternatively, some behavioral strategies are ubiquitous among populations of white-tailed deer: they exhibit crepuscular activity patterns throughout their range (Kammermeyer and

Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010). Although the daily light/dark cycles that influence diel activity are present across the range of white-tailed deer, other abiotic factors (e.g., weather and climate) are highly variable across the white-tailed deer's range. Deer in the northern United States and Canada contend with heavy snowfall and sub-zero temperatures during winter, while deer in the southern US rarely see snow, but are subject to high ambient temperatures and hurricanes. Understanding behavioral plasticity in deer is an important step in understanding the role behavior plays in their ability as a species to exploit such a wide range of environments.

Because the range of white-tailed deer is expansive and there is considerable variation among climatic, atmospheric, and weather patterns across this range, the behavioral responses of white-tailed deer to abiotic factors varies regionally as well. For example Beier and McCullough (1990) found that temperature had a strong influence on deer activity in all seasons in Michigan, but Pledger (1975) found no significant relationship between temperature and deer activity in southeastern Arkansas. The majority of investigations into deer activity relative to dynamic abiotic factors have been conducted in northern and Midwestern deer populations, and comparatively little is known about how abiotic factors influence activity in the Southeast. Our objective was to examine how abiotic factors influence activity patterns of white tailed deer in the Southeast. We hypothesized that adult deer in the Southeast would behave similarly to deer in other regions when adjusting activity relative to cyclical abiotic factors such as season, time of day, and moon phase, because these factors exert similar stresses across the range of white-tailed deer, and ecologically advantageous activity responses are likely similar across regions. Additionally, we expected to see greater regional plasticity in response to climatic factors, such

as temperature, weather condition, and wind speed, due to differing biological constraints among subspecies.

Methods

Study Area

We captured and collared all deer for this study on the northern portion of Brosnan Forest, a 5,830-ha tract of land owned by Norfolk Southern Railway, located in Dorchester County, South Carolina. The forested portion of the property was mainly comprised of mature longleaf pine (*Pinus palustris*) stands. Mixed pine-hardwood stands comprised of loblolly (*P. taeda*), slash (*P. elliottii*), and pond (*P. serotina*) pines; oak (*Quercus* spp.); sweetgum (*Liquidambar styraciflua*); and red maple (*Acer rubrum*) were also present in throughout the property. Drainages containing hardwood species including oak, sweetgum, black gum (*Nyssa sylvatica*), and yellow poplar (*Liriodendron tulipifera*) were interspersed throughout the property. Additionally, 126 ha of small food plots containing clover (*Trifolium* spp.), oats (*Avena sativa*), wheat (*Triticum aestivum*), rye (*Secale cereale*), chicory (*Cichorium intybus*), soybeans (*Glycine max*), and winter peas (*Pisum sativum*) were planted annually throughout the study area. Prescribed fire (2-3 year interval) maintained an open understory (Lauerman 2007; Collier et al. 2007) in upland areas. Supplemental corn and protein feeders were present throughout the study area at a density of approximately 1 feeder/50 ha.

Capture

We collared 116 adult deer (≥ 1 year old) during this study; 42 males from 2009-2011, 43 females from 2013-2015, and 31 deer (15 males and 16 females) from 2017-2018. We conducted captures on the 2,550-ha portion of Brosnan Forest located north of Highway 78. We sedated deer by injecting a pre-mixed dose of xylazine (Lloyd Laboratories, Shenandoah, Iowa;

100 mg/ml given at a rate of 2.2 mg/kg) and Telazol® (Fort Dodge Animal Health, Fort Dodge,

Iowa; 100 mg/ml given at a rate of 4.5 mg/kg). We injected the sedative intramuscularly using a

2 cc Type C Pneu-Dart propelled by a Pneu-Dart Model 389 tranquilizer gun (Pneu-dart Inc.,

Williamsport, Pennsylvania). We estimated the age of all deer using tooth replacement and wear

characteristics (Severinghaus 1949), and outfitted each deer with a GPS collar (Model G2110D;

Advanced Telemetry Systems, Isanti, Minnesota) weighing approximately 410 grams. We

affixed the collar to the neck of each deer and adjusted the fit to ensure collars remained in an

upright position to acquire accurate fixes (D'Eon and Delaparte 2005), while remaining loose

enough to allow for growth and prevent restriction. We allowed for additional growth and neck

enlargement during the breeding season by lining the collars fitted to males with a pliable foam

material. We injected a 3-ml intramuscular dose of Tolazoline (Lloyd Laboratories,

Shenandoah, Iowa; 100 mg/ml given at a rate of 6.6 mg/kg) to act as a reversal to the

xylazine/Telazol® mixture after we completed capture and collaring procedures, and at least 30

min had elapsed from the time we darted the deer. Following injection of the reversal agent, we

monitored deer from a distance until they moved away under their own power. These protocols

were approved by the Auburn University Animal Care and Use Committee (PRN#2008-1489,

PRN#2013-2205, PRN#2017-2996).

GPS Data Collection

　　During this study, the maximum period during which radio collars collected data varied

among years, lasting from 24 August through 23 November in 2009-2011, 16 August through 15

December in 2013-2015, and 1 August through 15 January of the following year in 2017 and

2018. The length of the collection period also varied among deer within the same year due to

collar malfunction, natural death, and hunter harvest. During the collection period, collars

attempted to record a GPS location every 30 min. We programed collars to automatically drop

off deer following the collection period. We then located collars using VHF radio telemetry.

Additionally, we retrieved all collars from hunter-harvested deer, and downloaded all collar-

collected data into Microsoft Excel using the ATS WinCollar software (Advanced Telemetry

Systems, Isanti, Minnesota). Data collected included GPS location recorded in UTM

coordinates, date, time, altitude, fix status, satellites, position dilution of precision (PDOP),

horizontal dilution of precision (HDOP), temperature, and activity sensor recording.

GPS Data Management

We assumed that the collection period did not include any capture-related behavioral

changes, because we darted all deer $\geq$ 18 days prior to the start of the collection period. We

removed three-dimensional GPS locations with a PDOP > 10 or an HDOP > 6 along with any 2-

dimensional fixes with an HDOP > 3 (D'Eon and Delparte 2005; Lewis et al. 2007).

Additionally, we visualized the data points using ArcMap 10.4.1 (Environmental Systems

Research Institute, Inc., Redlands, California, USA) and removed impossible or irrelevant fixes

(i.e., those recorded before or after the collection period and data points recorded after the deer

had died or the collar was no longer on the deer). Additionally, we excluded fixes that were

likely erroneous (e.g., a middle point of 3 successive fixes > 2,000 m outside the animal's home

range while the prior and successive fixes were closely associated with each other and within the

home range).

We used a two-state hidden Markov model in the *R* package momentuHMM to classify

each GPS location as either 'active' or 'inactive' following the example presented by

McClintock and Michelot (2018). The model used step length and turning angles to delineate

activity; inactive points had shorter step lengths and tighter turning angles, while active points

had longer step lengths and straighter paths. Additionally, we applied a maximum threshold distance between successive GPS locations that could be classified as inactive. To overcome potential biases associated with using thresholds from collars with differing accuracy, we used a conservative metric of four times the average error as a maximum threshold value between successive points for classifying GPS locations as inactive (Jerde and Visscher 2005; Sullivan et al. 2016). We considered all Euclidean distances between points greater than or equal to four times the average error distance as active. Accuracy tests revealed that collars deployed in the last two years of the study were substantially more accurate than those used in previous years, therefore we used threshold values of 51.78 m for 2009-2015 and 29.08 m for the 2017-2019 data. We derived these maximum distance thresholds from collar accuracy tests. To conduct these tests, we positioned test collars 1m above the ground (the approximate height of the neck of a white-tailed deer) with the antenna pointing vertically upward, and left them to collect GPS locations for approximately five days in different cover types found throughout the study area. We then compared the positional accuracy relative to the location of the collar as determined by a Trimble Geo 7X GPS (accurate to ≤ 1m). To reduce bias, we restricted activity classification to GPS locations collected at the scheduled 30-min intervals, and we excluded points from analyses when the inter-fix interval was longer than 30 min between successive locations.

Abiotic Factors

We obtained weather data from the monitoring station at Summerville Airport, Summerville, South Carolina (21.6 km southeast of the study area) via http://mesowest.utah.edu. Weather variables included barometric pressure, temperature, relative humidity, wind speed, wind direction, cloud cover, dew point, and a categorical weather condition classification. These abiotic factors were recorded at 20-min intervals. We used the weathermetrics *R* package to

convert temperature from Fahrenheit to Celsius, wind speed from miles per hour to meters per second, and to calculate relative humidity. We used the lunar package in program *R* to obtain moon phase for each day of the sampling period, and we obtained sunrise and sunset, and moonrise and moonset time for each day at Brosnan Forest (33°09'18.1"N, 80°25'44.5"W) using the suncalc package in program *R*. We approximated moon overhead and moon underfoot times by calculating the midpoint between moonrise and moonset, and the midpoint between moonset and the next moonrise, respectively.

Since deer are crepuscular (Hahn 1949, Montgomery 1963, Michael 1970, Kammermeyer and Marchinton 1977, Beier and McCullough 1990), we separated the day into four periods: morning, daytime, evening, and nighttime. To test for the optimal length of each period, we created nine candidate models using different period lengths surrounding sunrise and sunset to predict the odds of activity during any 30-min interval. We compared these models using AICc (Burnham and Anderson 2002) (Table 2.1). The top model classified morning as 1.5 hours before sunrise until 1.5 hours after sunrise, and evening as 1.5 hours before sunset until 1.5 hours after sunset. Daytime and nighttime were classified as the remaining times between the end of the morning and the beginning of the evening period, and between the end of the evening period and the beginning of the morning period respectively. We defined three sampling periods (pre-breeding, breeding, and post-breeding) based upon reproductive data from the study area. Our classification of the breeding season accounted for 80% of the conceptions on Brosnan Forest and lasted from 19 September until 28 October (McCoy et al. 2013). Due to the variation in start and end dates of data collection among years, the length of the pre-breeding, and post-breeding periods varied among years. We classified all data collected before and after the breeding period as the pre-breeding and post-breeding periods, respectively. Moon rise, moon

set, moon overhead, and moon underfoot periods were assigned using the method of Sullivan et al. (2016), where the moon rise period lasted from 2 hours before until 1.5 hours after moon rise, and moon overhead, moon set, and moon underfoot each lasted from 2 hours before until 1 hour after the moon overhead, moon set, and moon underfoot times.

For all numerical abiotic factors except barometric pressure, we matched the GPS location to the each abiotic factor recorded at nearest time to the time the GPS location was recorded. Barometric pressure is often used as an indicator of weather condition, where low pressure is generally associated with inclement weather, and high barometric pressure often indicates fair weather. Additionally, the rate of change in barometric pressure can indicate changes in weather, and faster rates of change are generally associated with more rapid changes in weather. To determine which metric of barometric pressure was a better predictor of deer movement, we used the entire dataset to compare competing metrics of barometric pressure. The only change between models was the metric used for barometric pressure, the base model included sex, season, diel period, and a random effect of individual. The metrics of barometric pressure included: the current barometric pressure at the time each GPS location was recorded, rate of change in barometric pressure over the four hours prior to the time each GPS location was recorded, the rate of change in barometric pressure over the past twenty-four hours prior to the time each GPS location was recorded, and a null model that did not include barometric pressure. The four-hour rate of change in barometric pressure had a much lower AIC value than all competing models (Table 2.2), therefore we used four-hour rate of change in barometric pressure for our abiotic predictor variable in the following barometric pressure analyses.

Data Analysis

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Since our response variable was binary (active or inactive), we used logistic regression to analyze the likelihood a deer would be active using a generalized linear mixed model for each categorical abiotic factor (wind direction, weather condition, moon phase, and moon position). To analyze continuous abiotic factors (wind speed, temperature, relative humidity, and barometric pressure), we used a generalized additive modeling (GAM) approach due to the flexibility of GAMs to model non-linear effects. It is well established that deer activity varies among seasons (pre-breeding, breeding, and post-breeding; Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010, Masse and Côté 2013) and time of day (Montgomery 1963, Michael 1970, Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010). Additionally, many of the abiotic factors we considered also vary seasonally and fluctuate in a cyclical nature on a daily basis. Therefore, we analyzed each time of day within each season separately. Due to differing constraints related to body size and behavioral differences among sexes (Webb et al. 2010), we included an interaction term for sex in all models. Additionally, to account for potential differences among individual deer, we applied a random effect of individual in all models. All analyses were conducted in program R (v3.5.2; R Core Development Team 2018).

Results

We captured 116 deer over the course of this study, of these, 9 were removed due to collar malfunctions or death prior to the collection period. We used 489,021 GPS locations collected from the 107 remaining deer (54 males and 53 females) for the following analyses. The probability of activity was greater for males (P_{Active} = 0.55; SE = 0.0011) than females (P_{Active} = 0.49; SE = 0.00097) on average. Additionally, probability of activity varied with season and time of day. The probability of activity was greatest during the breeding season

($P_{Active} = 0.57$; SE = 0.0012), followed by the post-breeding season ($P_{Active} = 0.52$; SE = 0.0013), and pre-breeding season ($P_{Active} = 0.47$; SE = 0.0013). The greatest probability of activity occurred during the evening ($P_{Active} = 0.78$; SE = 0.0017), followed by the morning ($P_{Active} = 0.65$; SE = 0.0020), night ($P_{Active} = 0.62$; SE = 0.0011), and was considerably less during the day ($P_{Active} = 0.26$; SE = 0.0011).

Temperature

In the pre-breeding season, adult male activity showed the most variation with respect to temperature during the morning and evening (Figure 2.1). In the morning, estimated probability of activity was generally greater during colder temperatures and decreased with warming temperatures, reaching lowest estimated value at 24°C ($P_{Active} = 0.66$; SE = 0.043), and stayed the same, or slightly increased, at greater temperatures. In the evening, probability of activity peaked at 21°C ($P_{Active} = 0.88$; SE = 0.021), decreasing during lower observed temperatures and higher observed temperatures up to 29°C ($P_{Active} = 0.63$; SE = 0.042), and then increased at temperatures greater than 29°C.

During the breeding season, male activity differed with temperature during the day and evening (Figure 2.2). Daytime probability of activity decreased as temperature increased, with estimated values of 0.46 (SE = 0.027), 0.41 (SE = 0.026), and 0.36 (SE = 0.027) at 10, 20, and 30°C, respectively. Probability of activity in the evening was greatest at 15°C ($P_{Active} = 0.92$; SE = 0.016) and steadily decreased to its lowest estimated value at 30°C ($P_{Active} = 0.80$; SE = 0.032). Evening activity tended to decrease at temperatures less than 15°C and increase at temperatures above 30°C.

During the post-breeding season, probability of male activity was most affected by temperature during the daytime (Figure 2.3). At observed daytime temperatures of 10°C or

greater, probability of activity did not vary, but at temperatures less than 10ºC probability of

activity increased as temperatures decreased with estimated values of 0.42 (SE = 0.031), 0.60

(SE = 0.032), and 0.71 (SE = 0.040) at 10, 0, and -5ºC respectively. The probability of activity

during the morning and night showed a similar trend, where observed temperatures greater than

~0ºC did not differ, but decreased with decreasing temperatures below ~0ºC.

In the pre-breeding season, adult female activity differed with respect to temperature

during the morning, evening, and night (Figure 2.4). In the morning, estimated probability of

activity was least at 24ºC (P_{Active} = 0.62; SE = 0.055), and increased with temperatures greater

and less than this point. In the evening, probability of activity generally decreased with

increasing temperatures, with a more pronounced decrease in estimated probability of activity

between 26ºC and 30ºC. At night, probability of activity increased from 0.66 (SE = 0.041) at

24ºC to 0.79 (SE = 0.034) at 29ºC, but probability of activity below 24ºC and above 29ºC were

steady.

During the breeding season, female activity varied with temperature during the day,

evening, and night time periods (Figure 2.5). Daytime probability of activity decreased as

temperatures increased with estimated values of 0.57 (SE = 0.047), 0.42 (SE = 0.044), and 0.31

(SE = 0.040) at 10, 20, and 30ºC, respectively. In the evening, probability of activity was greatest

from 12ºC (P_{Active} = 0.90; SE = 0.021) to 25ºC (P_{Active} = 0.89; SE = 0.021) and declined at

temperatures outside of this range. At night, probability of activity increased as temperatures

increased with estimated values of 0.82 (SE = 0.026), 0.85 (SE = 0.023), and 0.91 (SE = 0.019)

at 10, 20, and 30ºC, respectively.

In the post-breeding season, temperature affected probability female of activity in all four

diel periods (Figure 2.6). The morning and night periods showed a similar trend of greater

probability of activity at greater temperatures. Daytime probability of activity showed the

opposite trend, with estimated values of 0.67 (SE = 0.053), 0.60 (SE = 0.054), 0.45 (SE = 0.056),

and 0.34 (SE = 0.053) at -5, 0, 10, and 20°C respectively. In the evening, probability of activity

was greatest from 3°C (P_{Active} = 0.89; SE = 0.025) to 20°C (P_{Active} = 0.90; SE = 0.022) and

declined at temperatures outside of this range.

Relative Humidity

In the pre-breeding season, relative humidity had little effect on probability of adult male

activity during the morning, day, and night diel periods, although probability of activity

decreased slightly as relative humidity increased (Figure 2.7). In the evening, probability of

activity was least between 47% (P_{Active} = 0.64; SE = 0.042) and 70% (P_{Active} = 0.64; SE = 0.043)

relative humidity and increased outside of this range to values of 0.78 (SE = 0.033) and 0.82 (SE

= 0.028) at 35% and 100% respectively. Probability of male activity was generally stable with

changing relative humidity values in all diel periods during the breeding (Figure 2.8) and post-

breeding (Figure 2.9) seasons.

Probability of female activity varied with relative humidity at night during the pre-

breeding season (Figure 2.10), and tended to decrease with increasing relative humidity, with

estimated values of 0.90 (SE = 0.035) and 0.65 (SE = 0.042) at 40% and 100% relative humidity,

respectively; additionally, a localized peak occurred at 85% (P_{Active} = 0.73; SE = 0.036). During

the breeding season, probability of activity differed with relative humidity during the day,

evening, and night diel periods (Figure 2.11). Probability of activity during the morning was

stable when relative humidity was 60% or greater, and decreased when relative humidity was

less than 60%. During the day, probability of activity was least at 58% (P_{Active} = 0.31; SE =

0.041) and increased with increasing distance from 58% relative humidity, peaking at 27%

($P_{Active} = 0.65$; SE = 0.050) and 100% ($P_{Active} = 0.50$; SE = 0.045), the least and greatest observed

values. In the evening, probability of activity was least at 52% relative humidity ($P_{Active} = 0.82$;

SE = 0.033). There was a slight decreasing trend in nighttime probability of activity as relative

humidity increased, with estimated values of 0.95 (SE = 0.015), 0.91 (SE = 0.015), 0.88 (SE =

0.019), and 0.84 (SE = 0.023) at 40%, 60%, 80% and 100% relative humidity respectively.

During the post-breeding season, female activity was generally stable with changing values of

relative humidity (Figure 2.12).

Wind Speed

Probability of adult male activity during the pre-breeding season did not fluctuate

substantially during the morning, day, and evening periods (Figure 2.13). At night, probability

of activity was consistent from 0 to 28 km/hr and increased with increasing wind speeds greater

than 28 km/hr. In the breeding season there was little difference in probability of activity

associated with wind speed (Figure 2.14). During the post-breeding season, there was a general

decrease in activity with increasing wind speed during the morning and night periods (Figure

2.15). Estimated probability of morning activity was 0.92 (SE = 0.017), 0.90 (SE = 0.021), and

0.88 (SE = 0.027) at 0, 10, and 20 km/hr respectively. At night, probability of activity was

consistent from 0 to 20 km/hr and decreased with increasing wind speeds greater than 20 km/hr.

In the pre-breeding season, probability of female activity was affected by wind speeds

during the morning, evening, and night (Figure 2.16). In the morning, probability of activity was

slightly greater at 0 km/hr ($P_{Active} = 0.69$; SE = 0.048) than 5 km/hr ($P_{Active} = 0.64$; SE = 0.053),

and above 5 km/hr, probability of activity increased as wind speed increased, with estimated

probability of activity of 0.67 (SE = 0.050), 0.70 (SE = 0.054), and 0.76 (SE = 0.066) at 10, 20,

and 30 km/hr respectively. In the evening, estimated probability of activity decreased from 0.78

(SE = 0.034) at 0 km/hr to 0.67 (SE = 0.045) 10 km/hr and did not fluctuate substantially at observed winds speeds greater than 10 km/hr. At night, activity decreased with increasing wind speed from 5 km/hr (P_{Active} = 0.69; SE = 0.039) to 20 km/hr (P_{Active} = 0.55; SE = 0.055), and was relatively stable at wind speeds greater than 20 km/hr. Variation in probability of adult female activity with respect to wind speed was most evident at night during the breeding season, where model estimated probability of activity declined as wind speed increased, with a minor decrease in probability of activity between 5 km/hr (P_{Active} = 0.85; SE = 0.022) and 11 km/hr (P_{Active} = 0.79; SE = 0.030), and a sharper decrease in probability of activity at speeds greater than 20 km/hr (Figure 2.17). During the post-breeding season, probability of activity decreased with increasing wind speed at night (Figure 2.18), and estimated probability of nighttime activity was 0.82 (SE = 0.027), 0.79 (SE = 0.032), and 0.74 (SE = 0.039) at 0, 15, and 30 km/hr respectively.

Wind Direction

During the pre-breeding season, the probability of adult male deer activity differed with wind direction during the morning, day, and night (Figure 2.19). The greatest variation in activity with respect to wind direction occurred in the morning, where probability of activity ranged from 0.44 (SE = 0.043) to 0.76 (SE = 0.040), and males were most likely to be active during south (P_{Active} = 0.71; SE = 0.039) and southeast (P_{Active} = 0.76; SE = 0.40) winds and least likely during southwest (P_{Active} = 0.44; SE=0.063) and east (P_{Active} = 0.45; SE = 0.079) winds. During the day, male activity was greatest during east (P_{Active} = 0.25; SE = 0.025), southeast (P_{Active} = 0.24; SE = 0.028), south (P_{Active} = 0.23; SE = 0.022), and northwest (P_{Active} = 0.23; SE = 0.026) winds , and was least when winds blew from the northeast (P_{Active} = 0.17; SE = 0.018), and north (P_{Active} = 0.18; SE = 0.018). At night, males were more likely to be active when winds

were blowing from the west ($P_{Active} = 0.75$; SE = 0.028) compared to the east ($P_{Active} = 0.64$; SE = 0.029; $P = 0.005$) and northeast ($P_{Active} = 0.65$; SE = 0.029; $P = 0.032$).

During the breeding season, male activity relative to wind direction only differed in the evening (Figure 2.19), where they were more likely to be active during north ($P_{Active} = 0.83$; SE = 0.015; $P = 0.039$) and southeast ($P_{Active} = 0.85$; SE = 0.017; $P = 0.015$) winds compared to south winds ($P_{Active} = 0.78$; SE = 0.021).

Male activity during the post-breeding season differed with wind direction during the day and evening (Figure 2.19). During the day, probability of activity was greater during east ($P_{Active} = 0.28$; SE = 0.038) winds compared to southwest ($P_{Active} = 0.19$; SE = 0.026; $P = 0.007$) and southeast ($P_{Active} = 0.18$; SE = 0.032; $P = 0.037$) winds. In the evening, the probability of male activity ranged from 0.72 (SE = 0.030) during southwest winds to 0.82 (SE = 0.028) during southeast winds.

Adult female activity differed with wind direction during the day, evening, and night periods during the pre-breeding season (Figure 2.20). Probability of activity for females during the day was greater during southeast ($P_{Active} = 0.33$; SE = 0.028), south ($P_{Active} = 0.29$; SE = 0.024), east ($P_{Active} = 0.31$; SE = 0.026), and northwest ($P_{Active} = 0.28$; SE = 0.026) winds than north ($P_{Active} = 0.24$; SE = 0.021), southwest ($P_{Active} = 0.23$; SE = 0.021), northeast ($P_{Active} = 0.22$; SE = 0.021), and west ($P_{Active} = 0.22$; SE = 0.021) winds. In the evening, probability of activity was greatest during southeast ($P_{Active} = 0.75$; SE = 0.022) winds and least during north ($P_{Active} = 0.67$; SE = 0.026) winds. At night, probability of activity was least when winds were from the west ($P_{Active} = 0.41$; SE = 0.037) and greatest during south ($P_{Active} = 0.57$; SE = 0.029) winds.

During the breeding season, female activity differed among wind direction during the morning, evening, and night (Figure 2.20). In the morning, the probability of female activity was

significantly greater during south (P_{Active} = 0.77; SE = 0.029) compared to northeast (P_{Active} = 0.62; SE = 0.031) and north winds (P_{Active} = 0.65; SE = 0.031). In the evening, females were more likely to be active during east (P_{Active} = 0.89; SE = 0.015) compared to northeast (P_{Active} = 0.82; SE = 0.019; P = 0.047) winds. At night, females were most likely to be active during south (P_{Active} = 0.70; SE = 0.023) and west (P_{Active} = 0.68; SE = 0.028) winds and least likely to be active during northeast (P_{Active} = 0.57; SE = 0.025), north (P_{Active} = 0.58; SE = 0.023), and northwest (P_{Active} = 0.59; SE = 0.029) winds.

In the post-breeding season, the probability of female activity differed with wind direction during the day, evening, and night (Figure 2.20). Daytime activity ranged from 0.14 (SE = 0.018) to 0.24 (SE = 0.026) and tended to be greatest when winds were more northerly and least when they were coming from more southerly directions with estimated values of 0.24 (SE = 0.026), 0.23 (SE = 0.023), and 0.22 (SE = 0.024) for northwest, north, and northeast respectively, and 0.14 (SE = 0.018), 0.15 (SE = 0.019), and 0.18 (SE = 0.025) when winds were coming from the south, southwest, and southeast respectively. In the evening, probability of female activity ranged from 0.73 (SE = 0.024) to 0.82 (SE = 0.023) and was greater during north (P_{Active} = 0.80; SE = 0.016; $P \leq 0.001$) and southeast (P_{Active} = 0.82; SE = 0.023; P = 0.025) winds compared to west (P_{Active} = 0.73; SE = 0.024) winds. At night, female activity was greater during northwest (P_{Active} = 0.58; SE = 0.028) than during north winds (P_{Active} = 0.52; SE = 0.025).

Barometric Pressure

In the pre-breeding season, adult male activity changed with barometric pressure rate in all four diel periods (Figure 2.21). In the morning, probability of activity peaked when barometric pressure was stable (P_{Active} = 0.75; SE = 0.034), then decreased sharply as the rate of change in barometric pressure became increasingly positive, reaching low point at 0.26 mb/hr

(P_{Active} = 0.56; SE = 0.050). During the day, probability of activity was greatest when barometric

pressure was decreasing rapidly and least when barometric pressure was increasing rapidly, with

the greatest and least estimated probability of activity occurring at -0.81 mb/hr (P_{Active} = 0.21; SE

= 0.096) and 0.71 mb/hr (P_{Active} = 0.10; SE = 0.060), respectively. Evening probability of

activity was generally less when barometric pressure was decreasing rapidly and greater when

barometric pressure was increasing rapidly. Additionally, probability of activity decreased when

change in barometric pressure was near 0, with a localized minimum at -0.08 mb/hr (P_{Active} =

0.57; SE = 0.046). At night, probability of activity peaked at -0.33 mb/hr (P_{Active} = 0.86; SE =

0.016) and decreased steadily as the change in barometric pressure became greater. Probability

of adult male activity during the breeding season varied in the evening (Figure 2.22), with

estimated activity greatest at -0.47 mb/hr (P_{Active} = 0.92; SE = 0.015) and 0.19 mb/hr (P_{Active} =

0.90; SE = 0.019), and least at -0.06 mb/hr (P_{Active} = 0.79; SE = 0.034). In the post-breeding

season, probability of male activity differed most during the day and evening (Figure 2.23).

Daytime activity was greatest when the rate of change in barometric pressure was close to 0,

reaching a maximum of 0.50 (SE = 0.032) at -0.11 mb/hr, and decreasing as rate of change in

barometric pressure became increasing positive and negative. In the evening, activity was

generally less likely when barometric pressure was stable, with the minimum estimate at -0.08

mb/hr (P_{Active} = 0.84; SE = 0.030), and greatest when barometric pressure neared the most rapidly

increasing 0.80 mb/hr (P_{Active} = 0.98; SE = 0.010) and decreasing -0.70 mb/hr (P_{Active} = 0.95; SE

= 0.013) observed values.

Probability of adult female activity differed with rate of change in barometric pressure in

all four diel periods during the pre-breeding period (Figure 2.24). In the morning, probability of

activity was least when barometric pressure was rising at a rate of 0.24 mb/hr (P_{Active} = 0.62; SE

= 0.055). During the day, probability of activity increased with more rapidly decreasing barometric pressure and decreased with greater rates of increase in barometric pressure with estimates of 0.19 (SE = 0.043), 0.15 (SE = 0.033), and 0.10 (SE = 0.033) of at -0.5, 0, and 0.5 mb/hr respectively. In the evening, probability of activity was greatest at 0.18 mb/hr (P_{Active} = 0.79; SE = 0.032) and was greater when barometric pressure was rising compared to when it was falling. At night probability of activity decreased when barometric pressure was dropping faster than -0.34 mb/hr (SE = 0.044).

In the breeding season, probability of activity differed with barometric pressure during the day, evening, and night (Figure 2.25). During the day, females were least likely to be active when the rate of barometric pressure change was closer to -0.44 mb/hr (P_{Active} = 0.33; SE = 0.043) and 0.09 (P_{Active} = 0.32; SE = 0.041), and most likely to be active at -0.93 mb/hr (P_{Active} = 0.65; SE = 0.095), -0.17 mb/hr (P_{Active} = 0.44; SE = 0.044), and 0.48 mb/hr (P_{Active} = 0.47; SE = 0.055). Probability of evening activity was greatest when barometric pressure was falling most rapidly and when it was rising relatively slowly, and was least when the rate of change in barometric pressure was -0.21 mb/hr (P_{Active} = 0.84; SE = 0.031). At night, probability of activity was less when barometric pressure was decreasing more rapidly compared to when it was stable or increasing more rapidly, with estimated values of 0.79 (SE = 0.030), 0.84 (SE =0.023), and 0.88 (SE = 0.018) at -0.6, 0, and 0.6 mb/hr respectively.

In the post-breeding season, probability of adult female activity differed with barometric pressure in the day and evening (Figure 2.26). During the day, probability of activity was slightly greater when barometric pressure was rising compared to when it was steady or falling, with estimated values 0.35 (SE = 0.054), 0.37 (SE =0.054), and 0.45 (SE = 0.059) at -0.5, 0, and 0.5 mb/hr respectively. Likewise, probability of activity in the evening was greater when

barometric pressure was rising with the greatest estimated probability of activity occurring at 0.11 mb/hr (P_{Active} = 0.93; SE = 0.016), and the least occurring at -0.38 mb/hr (P_{Active} = 0.77; SE = 0.047).

Weather Condition

Detailed weather condition data were only available during 2013-2019, therefore we excluded the first three years of data from these analyses using only the 53 females and 15 males captured since those data records began. Additionally, we did not include fog during evening due to low sample sizes in the pre-breeding (n = 22) and breeding seasons (n = 21). In general, deer activity increased during precipitation in the daytime and decreased during precipitation at night and showed more consistent trends with females. Probability of activity during the morning and evening periods showed minimal changes and inconsistent trends relative weather condition among sexes and seasons.

In the pre-breeding season, the probability of male activity varied among weather condition during the day and night (Figure 2.27). Male activity ranged from 0.17 (SE = 0.063) to 0.34 (SE = 0.048) and was generally greater when precipitation was falling during the day. At night, activity ranged from 0.58 (SE = 0.053) during rain to 0.69 (SE = 0.047) under foggy conditions.

During the breeding season, probability of male activity differed with weather condition during all diel periods (Figure 2.28). In the morning, activity was greater during clear (P_{Active} = 0.77; SE = 0.030) compared to foggy conditions (P_{Active} = 0.69; SE = 0.043; P = 0.037). During the day, the probability of activity was least under clear (P_{Active} = 0.29; SE = 0.048; P = 0.012) and cloudy (P_{Active} = 0.30; SE = 0.048; P = 0.025) skies and greatest during rain (P_{Active} = 0.38; SE = 0.059). In the evening, probability of activity was greater during clear (P_{Active} = 0.83; SE =

0.022) compared to cloudy (P_{Active} = 0.76; SE = 0.029; $P \leq 0.001$) conditions. At night, probability of activity ranged from 0.67 (SE = 0.040) during foggy conditions to 0.78 (SE = 0.027) during cloudy conditions.

During the post-breeding season, male activity differed with weather condition only during the night period (Figure 2.29), ranging from 0.57 (SE = 0.049) during rain to 0.65 (SE = 0.042) during cloudy conditions, and generally decreasing with increasing precipitation intensity.

During the pre-breeding season, female activity varied with weather condition during the day, evening, and night periods (Figure 2.30). During the day, probability of activity ranged from 0.23 (SE = 0.034) to 0.39 (SE = 0.028) and was greater during periods of precipitation. In the evening, activity was greater during clear conditions (P_{Active} = 0.77; SE = 0.015) compared to when it was cloudy (P_{Active} = 0.73; SE = 0.017; P = 0.002). At night, activity was greatest under clear skies (P_{Active} = 0.54; SE = 0.028) and least during rain (P_{Active} = 0.42; SE = 0.031) and showed a general decrease with increasing cloud cover and precipitation intensity.

In the breeding season female activity differed with weather condition during all periods of the day (Figure 2.31). In the morning, activity was greater during fog (P_{Active} = 0.72; SE = 0.021) than during clear skies (P_{Active} = 0.66; SE = 0.022; $P \leq 0.001$), cloudy skies (P_{Active} = 0.65; SE = 0.023; $P \leq 0.001$), and rain (P_{Active} = 0.64; SE = 0.031; P = 0.041). During the day, probability of activity ranged from 0.27 (SE = 0.023) under cloudy skies to 0.46 (SE = 0.039) while it was drizzling, and was greater during periods of precipitation. In the evening, probability of activity ranged from 0.82 (SE = 0.031) during drizzle to 0.88 (SE = 0.009) during clear skies. At night, activity was greatest under clear skies (P_{Active} = 0.63; SE = 0.020) and least during rain (P_{Active} = 0.50; SE = 0.026), and was generally less when precipitation was falling.

During the post-breeding season, probability of female activity differed with weather condition during the day, evening, and night (Figure 2.32). During the day, probability of activity ranged from 0.17 (SE = 0.027) during fog to 0.34 (SE = 0.036) during rain, and generally increased with increasing precipitation intensity. In the evening, probability of activity was greater during periods of clear skies (P_{Active} = 0.82; SE = 0.013) compared to cloudy skies (P_{Active} = 0.79; SE = 0.015; P = 0.009). At night, activity was greatest under cloudy skies (P_{Active} = 0.56; SE = 0.024) and least during rain (P_{Active} = 0.45; SE = 0.027) and was generally less when precipitation was falling compared to when it was not.

Moon Phase

In the pre-breeding season we found evidence that adult male activity differed across moon phase during the day, evening, and night (Figure 2.33). During the day, probability of activity was greatest during the first quarter (P_{Active} = 0.22; SE = 0.020), which was greater than the waning crescent (P_{Active} = 0.18; SE = 0.017; P = 0.002), new (P_{Active} = 0.18; SE = 0.018; P = 0.032), and full moon (P_{Active} = 0.18; SE = 0.017; $P \leq 0.001$). During the evening, probability of activity was greatest during the last quarter (P_{Active} = 0.74; SE = 0.020), and least during the waxing crescent (P_{Active} = 0.68; SE = 0.022). At night, probability of activity ranged from 0.64 (SE = 0.026) during the waxing gibbous to 0.70 (SE = 0.023) during the waning gibbous and tended to decrease closer to the waxing gibbous.

During the breeding season, male activity differed with moon phase during all four periods of the day (Figure 2.34). In the morning, probability of activity ranged from 0.75 (SE = 0.021) to 0.81 (SE = 0.017) and was greater during the waxing gibbous (P_{Active} = 0.81; SE = 0.017) compared to the waning gibbous (P_{Active} = 0.75; SE = 0.021; P = 0.013) and first quarter (P_{Active} = 0.76; SE = 0.020; P = 0.033). During the daytime, probability of activity was generally

less during the brighter moon phases and was least during waning gibbous (P_{Active} = 0.29; SE = 0.023), and greatest during the waning crescent (P_{Active} = 0.36; SE = 0.026). In the evening, probability of activity ranged from 0.80 (SE = 0.017) during the waning gibbous to 0.86 (SE = 0.014) during the waning crescent. At night, probability of activity was least during the new moon (P_{Active} = 0.74; SE = 0.018) and greatest during the full moon (P_{Active} = 0.81; SE = 0.014).

During the post-breeding season, adult male activity differed across moon phase in the day and night (Figure 2.35). During the day, probability of activity was greatest during the new moon (P_{Active} = 0.27; SE = 0.030) and was significantly less during the waxing gibbous (P_{Active} = 0.23; SE = 0.027; P = 0.020) and last quarter (P_{Active} = 0.23; SE = 0.027; P = 0.033). At night, probability of activity was greatest during the waxing gibbous (P_{Active} = 0.77; SE = 0.019) and full moon (P_{Active} = 0.75; SE = 0.020) and least during the first quarter (P_{Active} = 0.70; SE = 0.023).

In the pre-breeding season we found evidence that adult female activity varied among moon phase across all periods of the day (Figure 2.36). The greatest variation occurred during the night period, where probability of activity ranged from 0.48 (SE = 0.028) during the waning gibbous to 0.58 (SE = 0.027) during the waning crescent. Probability of activity tended to decrease closer to the full moon during the morning, evening, and night (Figure 1), and was least during the full moon (P_{Active} = 0.54; SE = 0.031) in the morning and the waxing gibbous during the evening (P_{Active} = 0.74; SE = 0.019) and night (P_{Active} = 0.48; SE = 0.028). Conversely, during the day, probability of activity was greatest during the first quarter (P_{Active} = 0.29; SE = 0.024) and least during the waning crescent (P_{Active} = 0.23; SE = 0.020) and tended to be slightly greater during the brighter moon phases.

During the breeding season, we found evidence that adult female activity varied among moon phase during all periods of the day (Figure 2.37). In the morning, probability of activity was greater during the new (P_{Active} = 0.69; SE = 0.022; $P \leq 0.001$) and waxing crescent (P_{Active} = 0.70; SE = 0.022, P = 0.001) compared to the waning crescent (P_{Active} = 0.61; SE = 0.026). Probability of daytime activity ranged from 0.24 (SE = 0.021) to 0.32 (SE = 0.024) and was least during the first quarter (P_{Active} = 0.24; SE = 0.021) and waning crescent (P_{Active} = 0.26; SE = 0.022), and greatest during the waning gibbous (P_{Active} = 0.30; SE = 0.023), last quarter (P_{Active} = 0.32; SE = 0.024), and waxing crescent (P_{Active} = 0.32; SE = 0.024). The greatest variation in probability of activity occurred at night, ranging from 0.57 (SE = 0.023) to 0.69 (SE = 0.020), tending to be greatest during the brighter phases and peaking at the full moon (P_{Active} = 0.69; SE = 0.020).

Following the breeding season adult female activity differed among moon phase during the morning, day, and night (Figure 2.38). In the morning, probability of activity was greatest during the full moon (P_{Active} = 0.67; SE = 0.028), and was less during the waning gibbous (P_{Active} = 0.57; SE = 0.031; $P \leq 0.001$) and last quarter (P_{Active} = 0.61; SE = 0.030; P= 0.046). During the day, probability of activity was similar through the first four phases, then dropped to its lowest estimated value during the full moon (P_{Active} = 0.15; SE = 0.018) then steadily increased, peaking at 0.24 (SE = 0.024) during the waxing crescent. Similar to the daytime trend, probability of nighttime activity did not differ among the first four moon phases, but in contrast to the daytime trend, probability of activity peaked during the full moon (P_{Active} = 0.60; SE = 0.024) and steadily decreased to its least during the waning crescent (P_{Active} = 0.52; SE = 0.026).

Moon Position

Male deer activity showed little variation among moon position in the pre-breeding season, and differed among moon position in the day and evening periods. During the day, probability of activity was greater during moon rise ($P_{Active} = 0.21$; SE = 0.018; $P = 0.043$) than moon underfoot ($P_{Active} = 0.18$; SE = 0.017; Figure 2.39). In the evening, probability of activity ranged from 0.68 (SE = 0.022) to 0.75 (0.021) and was greater during moon underfoot ($P_{Active} = 0.75$; SE = 0.021; $P = 0.009$) compared to moon set ($P_{Active} = 0.68$; SE = 0.022).

The probability of male activity differed with moon phase during the evening and night time periods of the breeding season (Figure 2.40). In the evening, males were least likely to be active during moon rise ($P_{Active} = 0.81$; SE = 0.015) and most likely to be active during moon set ($P_{Active} = 0.85$; SE = 0.013). At night, activity was greater during the moon rise ($P_{Active} = 0.79$; SE = 0.016) and moon overhead ($P_{Active} = 0.81$; SE = 0.015) periods compared to the moon set ($P_{Active} = 0.76$; SE = 0.017) and underfoot ($P_{Active} = 0.75$; SE = 0.018).

During the post-breeding season, male activity differed with moon position during the day and night (Figure 2.41). In the daytime, activity was greater during moon underfoot ($P_{Active} = 0.27$; SE = 0.030) than moon rise ($P_{Active} = 0.23$; SE = 0.026; $P = 0.003$). Probability of activity was greater during moon overhead ($P_{Active} = 0.77$; SE = 0.020) than moon rise ($P_{Active} = 0.72$; SE = 0.022; $P \leq 0.001$), moon set ($P_{Active} = 0.73$; SE = 0.022; $P = 0.005$), and moon underfoot ($P_{Active} = 0.71$; SE = 0.023; $P \leq 0.001$).

Female activity during the pre-breeding season differed among moon positions during the morning and night periods (Figure 2.42), ranging from 0.54 (SE = 0.031) to 0.62 (SE = 0.028) in the morning and 0.49 (SE = 0.028) to 0.55 (SE = 0.027) at night. The pattern of activity was similar among these two periods, with probability of activity least during the moon set during the morning ($P_{Active} = 0.54$; SE = 0.031) and night ($P_{Active} = 0.49$; SE = 0.028).

During the breeding season, female activity differed with moon phase in the morning, day, and night periods (Figure 2.43). In the morning, activity was greatest during the moon rise (P_{Active} = 0.69; SE = 0.021; P = 0.047) and least during the moon set (P_{Active} = 0.64; SE = 0.024). During the day, activity was greatest during moon rise (P_{Active} = 0.61; SE = 0.028) and moon underfoot (P_{Active} = 0.62; SE = 0.028) and least during the moon set (P_{Active} = 0.54; SE = 0.031). The probability of activity at night ranged from 0.59 (SE = 0.023) to 0.69 (SE = 0.020) and was greater during moon overhead (P_{Active} = 0.69; SE = 0.020) than moon rise (P_{Active} = 0.59; SE = 0.023; $P \le 0.001$), moon set (P_{Active} = 0.64; SE = 0.022; $P \le 0.001$), and moon underfoot (P_{Active} = 0.59; SE = 0.023; $P \le 0.001$).

During the post-breeding season, female activity differed among moon position during the day and at night (Figure 2.44). Daytime activity was greater during moon rise (P_{Active} = 0.22; SE = 0.024) and moon overhead (P_{Active} = 0.22; SE = 0.024) compared to moon set (P_{Active} = 0.19; SE = 0.022) and moon underfoot (P_{Active} = 0.19; SE = 0.022). At night, activity was greater during moon overhead (P_{Active} = 0.60; SE = 0.024) than moon rise (P_{Active} = 0.54; SE = 0.025; $P \le$ 0.001), moon set (P_{Active} = 0.54; SE = 0.026; $P \le 0.001$), and moon underfoot (P_{Active} = 0.53; SE = 0.026; $P \le 0.001$).

Discussion

Sex-related differences in activity, along with daily and seasonal activity trends observed here corroborate those of most other research (e.g., Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010). We observed that both sexes were more active during the breeding season, and males were typically more active than females. Sex-related differences reported here agree with others who have found that males are typically wider ranging and move more than females. For example, male home ranges are typically larger than females (DeYoung

and Miller 2011). Likewise, Webb et al. (2010) observed that males have greater daily movement distances and are more generally more active than females (Beier and McCullough 1990). Elevated activity during the breeding season, similar to what we observed, has been reported elsewhere for both males (Hellickson 2002) and females (Ivey and Causey 1981). Additionally, we observed that deer activity patterns were generally crepuscular, with the greatest probability of activity occurring during morning and evening. Furthermore, deer were more active at night than during the day. Similar crepuscular activity patterns in deer have been widely observed (Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Webb et al. 2010), with notable exceptions during the breeding season (Hellickson 2002) and in predator-free environments (Bonnot et al. 2016). The similarities between our results and data from other regions suggest that sex, season, and time of day influence activity similarly across the range of white-tailed deer.

Temperature

There seems to be a trend toward minimizing energetic losses by increasing activity in more thermally optimal diel periods, as has been observed in other deer species (Merrill 1991, Dussalt et al. 2004). Ambient temperatures observed during this study ranged from -11 to 37˚C. Demarais et al. (1986) observed that over a similar range of ambient temperatures (3-39˚C), adult deer rectal temperatures were associated positively with ambient temperature, with the greatest average rectal temperature occurring in late August and early September and the least rectal temperatures occurring in December. This may be indicative of thermal stress, which Demarais et al. (1986) speculated was occurring during the warmer periods (July-September). Rogers et al. (1987) observed similar changes in rectal temperatures, and reported that low and high ambient temperatures caused subtle shifts in white-tailed deer behavior that aided in

thermoregulation. For example, during the warmest periods of their study, white-tailed deer avoided direct sunlight, and during colder periods white-tailed deer bedded for longer periods and increased use of sunlit areas (Rogers et al. 1987). Additionally, Rogers et al. (1987) reported that physical exertion greatly increased rectal temperature during winter. Similarly, we observed that activity of both sexes decreased with increasing daytime ambient temperatures, and generally increased with increasing nighttime temperatures during the breeding and post-breeding seasons. This suggests that, similar to other deer species (Merrill 1991, Dussault et al. 2004), white-tailed deer in the Southeast adjust daily activity to more thermally optimal periods during the breeding and post-breeding seasons. However, the same trend was not evident during the pre-breeding season, which may be due to differences in seasonal isolative properties of deer pelage. White-tailed deer shed their summer coat and replace it with a more insulative winter coat in August and September (Sauer 1984). However, ambient temperatures on our study site frequently exceed 30°C into the breeding season and can exceed 25°C in the post-breeding season. Holter et al. (1975) observed that white-tailed deer panted, a behavior that reduces body temperature, at ambient temperatures of 30°C and greater during fall, and temperatures above 25°C caused increased energy expenditure due to heat stress. Additionally, Holter et al. (1975) noted that deer generally reduced time spent standing as ambient temperatures exceeded or dropped below 20°C. Our data suggest that deer adjust behaviorally to thermal stress caused by ambient temperatures, and suggest that ambient temperatures in South Carolina, and likely in the Southeast in general, is sufficient at times to cause deer to adjust activity.

Relative Humidity

Relative humidity had little effect on activity during the majority of the time periods we sampled, but in the pre-breeding season, both sexes tended to decrease activity with increasing

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relative humidity at night. Greater values of relative humidity can make thermoregulation by

evaporative heat loss mechanisms (e.g., sweating or panting) less effective. Additionally, in

colder temperatures greater relative humidity can make temperatures seem colder because

moisture in the air increases conduction of heat from the body. Accordingly, Beier and

McCullough (1990) observed a decrease in white-tailed deer activity at greater relative humidity

values during colder periods in Michigan. However, we did not observe a strong relationship

between activity and relative humidity during the post-breeding season, the coldest period

sampled. The lack of a consistent trend, and relatively slight changes in activity with differing

values of relative humidity agrees with prior investigations. For example Behrend (1966) and

Carbaugh et al. (1975) observed no relationship between relative humidity and activity or

roadside survey count data respectively. Webb et al. (2010) found that relative humidity had an

inconsistent effect on white-tailed deer activity. They observed female movement increased with

increasing relative humidity during spring but were unaffected in all other seasons, and males

decreased movement during spring and winter as relative humidity increased (Webb et al. 2010).

Additionally, Demarais et al. (1986) observed that relative humidity had no effect on white-tailed

deer body temperature in Mississippi. As in other regions, and in agreement with prior research

in the Southeast (Demarais et al. 1986), we observed that white-tailed deer do not demonstrate

consistent patterns of activity in response to relative humidity, which likely indicates that the

effect of relative humidity on deer activity in the Southeast is minimal.

Wind Speed

Wind speed affected females more than males, and had the greatest influence on female

activity at night, where probability of activity decreased as wind speed increased. Wind speed

can affect the ability of prey species to detect predators (Leuthold 1977, Cherry and Barton

2017). Auditory and olfactory senses can be negatively impacted by greater wind speeds, which

may be especially important at night when deer vision may also be impaired. Female activity is

more likely to be impacted by the decrease in predator detection associated with greater

nighttime wind speed compared to male activity because females and their fawns are more likely

to be predated in the Southeast (Labisky and Boulay 1998, Kilgo et al 2010, Kilgo et al. 2012,

Nelson et al. 2015, Kilgo et al. 2016). While not apparent during all seasons, there was some

evidence that male activity decreased as wind speed increased at night during the post-breeding

season. Male body condition is often compromised during the breeding season, and may lead to

a greater risk of natural mortality (Ditchkoff et al. 2001), which may be accompanied by an

increase in antipredator behaviors such as decreasing activity. Similarly, Gulsby et al. (2018)

observed that males were more vigilant in areas where coyotes were more abundant during the

post-breeding season (January-February), whereas vigilance was not affected by coyote

abundance during fall (October-November). Another possible explanation for decreasing

activity during greater wind speeds in the post-breeding season is that deer may remain inactive

to reduce the negative energetic effects of wind chill. Both Moen (1968) and Holter et al. (1975)

observed that greater wind speeds could act in conjunction with cold temperatures to increase

energy expenditure in white-tailed deer. However, white-tailed deer may be able to mediate the

negative effects of wind chill by bedding (Holter et al. 1975) or seeking shelter from wind

provided by terrain and vegetation (Moen 1968). Likewise Beier and McCullough (1990)

observed that white-tailed deer selected for closed forests rather than open areas on windier days

during winter.

Wind Direction

The influence of wind direction on deer activity was highly variable, and there were no discernable patterns among the data. Winds blowing from certain directions may be indicative of future or current weather conditions, and particular responses to certain wind directions may be advantageous. Due to the proximity to the Atlantic coast, winds on our study site may be influenced by both continental and coastal winds that differ seasonally (Weber and Blanton 1980, Martin and Konrad 2006). Prevailing winds often indicate stable weather conditions whereas winds coming from other directions indicate changing weather patterns. Winds predominantly come from the north, but often come from the south and west in the pre and post-breeding seasons (North Carolina Climate Office 2019). However, we observed that variation in activity was not consistent with prevailing or non-prevailing wind direction. Alternatively, olfaction is important for location of forage, predator detection, and social interactions of white-tailed deer (Ditchkoff 2011) and can be influenced by wind. Therefore, wind direction relative to the position of deer and the location of the source of a scent of interest (e.g., predators, food sources, and conspecifics) may be more important than whether the wind is blowing from a certain direction.

Barometric Pressure

We observed that change in barometric pressure was a better predictor of activity than barometric pressure at the time of each activity event, although patterns of activity relative to barometric pressure change were not consistent across sexes, seasons, or diel period in our study. Previous research that has examined the influence of barometric pressure on deer behavior has produced conflicting results. Hosey (1980), Pledger (1970), and Kammermeyer (1975) evaluated white-tailed deer activity relative to the current barometric pressure. Hosey (1980) found that barometric pressure did not influence white-tailed deer movement distance or activity.

However, Pledger (1970) and Kammermeyer (1975) observed a positive relationship between barometric pressure and white-tailed deer activity and movement rate, respectively. Changes in barometric pressure often precede shifts in weather patterns, and it would be advantageous for animals to use barometric pressure to predict future weather conditions. Birds and bats possess a paratympatic organ within their inner ear that enables them to sense small changes in barometric pressure (Paige 1995, von Bartheld and Giannessi 2011). The paraypmpatic organ may be used to sense changes in weather, however bats are the only mammals known to possess a paratympatic organ, and it is unclear what mechanism other mammals might use to sense changes in barometric pressure (Paige 1995, von Bartheld and Giannessi 2011). Nevertheless, Tomberlin (2006) and Tilton and Willard (1982) found a relationship between rate of barometric pressure change and behavior in ungulates. Tomberlin (2006) observed that white-tailed deer were most active when barometric pressure was stable and were less active as barometric pressure increased or decreased. Tilton and Willard (1982) found when barometric pressure was stable, bighorn sheep (*Ovis canadensis*) group size was greater than when barometric pressure was rising and falling.

Weather Condition

We observed minimal differences in deer activity relative to weather condition in the morning and evening periods, when deer are typically most active. Likewise, Webb et al. (2010) observed few differences in deer movement relative to weather variables during the crepuscular period. However, outside of these periods our data suggest that white-tailed deer activity is consistently affected by weather condition. Generally, we observed deer were less likely to be active when rain was falling at night, and more likely to be active when rain was falling during the day. It is possible that these patterns are due to the impact that rain has on their ability to

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thermoregulate. Parker (1988) found that black-tailed deer (*Odocoileus hemionus columbianus*) metabolic rate was affected by simulated rainfall during summer at temperatures below 10˚C, and energy expended during five hours of simulated rainfall in summer pelage was greater than black-tailed deer experiencing heat or cold stress. Our data suggest female activity decreased more than male activity during nighttime rain, and female activity increased more than male activity during daytime rain. Females and their fawns are more likely to be affected by weather-related thermal stress caused by rain as a consequence of their smaller body size (Moen 1968, Parker 1988).

Moon Phase

Nighttime activity was generally greatest during brighter moon phases during the breeding and post-breeding seasons for both sexes. These results agree with those of prior studies. Buss and Harbert (1950) observed that more mule deer used a salt lick during brighter moon phases. Likewise, Kammermeyer (1975) and Montague et al. (2017) observed greater white-tailed deer activity near the full moon, and deer-vehicle collision frequency increased near the full moon (Colino-Rabanal et al. 2018). However, others have found no relationship between deer behavior and moon phase (Zagata and Haugen 1974, Kufeld 1988, Beier and McCollough 1990, and Webb et al. 2010). Since moon phase affects nighttime brightness and deer vision is particularly well suited for crepuscular activity (D'Angelo 2008), different nocturnal visibility associated with brighter and darker moon phases may explain the moon phase effect we observed. However, moon position and weather condition also contribute to nighttime brightness. Therefore, considering moon phase alone may not capture the influence of nocturnal brightness, and the combined effect of moon phase, moon position, and weather conditions on brightness may lead to different conclusions among studies.

Interestingly, our data suggest that females were generally less active during brighter moon phases at night during the pre-breeding season, but more likely to be active during the breeding and post-breeding seasons. Contrasting relationships among seasons may be related to the effect of hunting pressure. Human hunters are the leading source of mortality for adult deer in the Southeast (Kilgo et al. 2016, Wiskirchen 2017). Accordingly, white-tailed deer respond to hunting pressure by adjusting spatially (Little et al. 2016, Sullivan et al. 2018) and temporally (Simoneaux 2015, Little et al. 2016, Wiskirchen 2017, Sullivan et al. 2018) to increased risk. Deer hunting on Brosnan Forest occurred during daylight hours from 15 September - 1 January (Sullivan et al. 2018), and coincided with the breeding and post-breeding seasons. Predation upon adults by natural predators is relatively rare in the Southeast (Labisky and Boulay 1998, Chitwood et al. 2014, Kilgo et al. 2016), but is common in fawns (Kilgo et al 2010, Kilgo et al. 2012, McCoy et al. 2013, Nelson et al. 2015). Risk associated with coyotes may also cause behavioral responses in female white-tailed deer in the Southeast, especially during fall (Cherry et al. 2015, Gulsby et al. 2018). Although deer may be able to detect predators better during brighter moon phases, coyotes may also be more effective hunters in brighter conditions (Wells 1978, Wells and Lehner 1978). Our data suggest that females may respond to greater risk to themselves or their fawns from natural predators during the pre-breeding season by decreasing activity during brighter moon phases. Alternatively, during the breeding and post-breeding seasons, when fawns are less vulnerable to natural predators, and adults are more vulnerable to daytime risk associated with human hunters, our data suggest that females are more active during brighter moon phases.

Moon Position

We observed greater nighttime activity when the moon was overhead, suggesting that white-tailed deer are more active during the brightest periods of the night, in the breeding and post-breeding seasons. Likewise, Colino-Rabanal (2018) found that vehicle collisions with white-tailed deer occurred most often during the time of night when the moon was bright, and least during moonless periods. The visual acuity hypothesis presented by Prugh and Golden (2014) states that prey that rely on vision should increase their activity during brighter nighttime conditions because greater nocturnal brightness should improve foraging efficiency and predator detection. An alternative explanation is that pressure changes associated with moon phase affect deer activity, and there is greater atmospheric pressure during periods when the moon is overhead or underfoot (Kohyama and Wallace 2014). In aquatic ecosystems, the influence of moon position on organisms is well documented due to tidal changes. However, a mechanism to explain the effect of slight pressure changes associated with moon position on white-tailed deer is obscure. Our data suggest that the effect of moon position is more consistent with increased nocturnal light and the visual acuity hypothesis rather than changes in atmospheric tides. However, the differences we observed between probability of activity during the brightest and darkest moon positions were modest.

Literature Cited

Ayeni, J. S. O. 1975. Utilization of waterholes in Tsavo National Park (East). East African Wildlife Journal 13:305-323.

Behrend, D. F. 1966. Correlation of white-tailed deer activity, distribution, and behavior with climatic and other environmental factors. New York Department of Conservation, Job Completion Report. 123pp.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs 109:3-51.

Bonnot, N. C., N. Morellet, A. J. M. Hewison, J-L. Martin, S. Benhamou, and S. Chaamaillé-Jammes. 2016. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm to the absence of predators. Canadian Journal of Zoology 94:385-394.

Buss, I. O., and F. H. Harbert. 1950. Relationship of moon phase to the occurrence of mule deer at a salt lick. Journal of Mammalogy 31:426-429.

Carbaugh, B., J. P. Vaughan, E. D. Bellis, and H. B. Graves. 1975. Distribution and activity of white-tailed deer along an interstate highway. Journal of Wildlife Management 39:570-581.

Cherry, M. J., L. M. Conner, and R. J. Warren. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26: 1091-1099.

Cherry, M. J., and B. T. Barton. 2017. Effects of wind on predator-prey interactions. Food Webs 13:92-97.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2014. Confirmation of

coyote predation on adult female white-tailed deer in the southeastern United States. Southeastern Naturalist 13:30-32.

Colino-Rabanal, V. J., T. A. Langen, S. H. Peris, and M. Lizana. 2018. Ungulate:vehicle collision rates are associated with the phase of the moon. Biodiversity and Conservation 27:681-694.

Collier, B. A., S. S. Ditchkoff, J. B. Raglin, and J. M. Smith. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. Journal of Wildlife Management 71:277-281.

D'Angelo, G. J., A. Glasser, M. Wendt, G. A. Williams, D. A. Osborn, G. R. Gallagher, R. J. Warren, K. V. Miller, and M. T. Pardue. 2008. Visual specialization of an herbivore prey species, the white-tailed deer. Canadian Journal of Zoology 86:735-743.

de Lamo, D. A., A. F. Sanborn, C. D. Carrasco, and D. J. Scott. 1998. Daily activity and behavioral thermoregulation of the guanaco (*Lama guanicoe*) in winter. Canadian Journal of Zoology 76:1388-1393.

Demarais, S., J. W. Fuquay, and H. A. Jacobson. 1986. Seasonal rectal temperatures of white-tailed deer in Mississippi. Journal of Wildlife Management 50:702-705.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383-388.

DeYoung, C. A. 2011. Population Dynamics. Pages 147-180 in D. G. Hewitt (ed.). Biology and management of white-tailed deer. Taylor and Francis Group, Boca Raton, FL.

DeYoung, R. W., and K. V. Miller. 2011. White-tailed deer behavior. Pages 311-354 in D. G. Hewitt (ed.). Biology and management of white-tailed deer. Taylor and Francis Group, Boca Raton, FL.

Ditchkoff, S. S., E. R. Welch Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed deer support mate-competition theory. Journal of Wildlife Management 65:552-559.

Ditchkoff, S. S. 2011. Anatomy and Physiology. Pages 43-74 in D. G. Hewitt (ed.). Biology and management of white-tailed deer. Taylor and Francis Group, Boca Raton, FL.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal condition in the boreal forest. Ecoscience 11:321-328.

Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist 133:36-43.

Gulsby, W. D., M. J. Cherry, J. T. Johnson, L. M. Conner, and K. V. Miller. 2018. Behavioral response of white-tailed deer to coyote predation risk. Ecosphere 9(3):e02141.10.1002/ecs2.2141.

Hahn, H. C. 1949. A method of censusing deer and its application in the Edwards Plateau of Texas. Division of Wildlife Restoration, Texas Game, Fish, and Oyster Commission, Austin. 24 pp.

Hellickson, M. W. 2002. Age-specific physical characteristics, activity, and behavior patterns of male white-tailed deer in southern Texas. Dissertation, University of Georgia, Athens, Georgia, USA.

Huegel, C. N., and O. J. Rongstad. 1985. Winter foraging patterns and consumption rates of northern Wisconsin coyotes. Am. Midl. Nat., 113:203-207.

Holter, J. B., W. E. Urban, H. H. Hayes, H. Silver, and H. R. Skutt. 1975. Ambient temperature effects on physiological traits of white-tailed deer. Canadian Journal of Zoology 53:679-685.

Hosey, A. G. Jr. 1980. Activity patterns and notes on the behavior of male white-tailed deer during the rut. Thesis, Auburn University, Auburn, Alabama, USA.

Ivey, T. L., and M. K. Causey. 1981. Movements and activity patterns of female white-tailed deer during rut. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 35:149-166.

Jacobsen, N. K. 1980. Differences of thermal properties of white-tailed deer pelage between seasons and body regions. Journal of Thermal Biology 5:151-158.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parameterization. Ecological Applications 15:806-810.

Johns, P. E., M. H. Smith, and R. K. Chesser. 1984. Annual cycles of kidney fat index in a Southeastern white-tailed deer herd. Journal of Wildlife Management 48:969-973.

Kammermeyer, K. E. 1975. Movement-ecology of white-tailed deer in relation to a refuge and hunted area. Thesis, University of Georgia, Athens, Athens, Georgia, USA.

Kammermeyer, K. E., and R. L. Marchinton. 1977. Seasonal change in circadian activity of radio-monitored deer. Journal of Wildlife Management. 41:315-317.

Kilgo, J. C., H. S. Ray, C. R. Ruth, and K. V. Miller. 2010. Can coyotes affect deer populations in Southeastern North America? Journal of Wildlife Management 74:929-933.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420-1430.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747-753.

Kohyama, T., and J. M. Wallace. 2014. Lunar gravitational atmospheric tide, surface to 50 km in a global, gridded data set. Geophysical Research Letters 41:8660-8665.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1988. Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. Journal of Range Management 41:515-522.

Labisky, R. F., and M. C. Boulay. 1998. Behaviors of bobcats preying on white-tailed deer in the Everglades. The American Midland Naturalist 139:275-281.

Lauerman, S. 2007. Effects of season of fire on red cockaded woodpecker (*Picoides borealis*) reproduction and the breeding bird community of a longleaf pine ecosystem. Thesis, Clemson University, Clemson, South Carolina USA.

Leuthold, W. 1977. African ungulates: a comparative review of their ethology and behavioral ecology. Springer-Verlag, New York, New York.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

Little, A. R., S. L. Webb, S. Demarais, K. L. Gee, S. K. Riffell, and J. A. Gaskamp. 2016. Hunting intensity alters movement behaviour of white-tailed deer. Basic and Applied Ecology 360-369.

Martin, J., and Konrad, C. 2006. Directional characteristics of potentially damaging wind gusts in the southeast United States. Physical Geography 27:155-169.

Massé, A., and S. D. Coté. 2013. Spatiotemporal variations in resources affect activity and

    movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density.

    Canadian Journal of Zoology 91:252-263.

McClintock, B. T., and T. Michelot. 2018.momentuHMM: R package for generalized hidden

    Markov models of animal movement. Methods in Ecology and Evolution 9:1518-1530.

McCoy, J. C., S. S. Ditchkoff, J. B. Raglin, B. A. Collier, and C. Ruth. 2013. Factors influencing

    survival of white-tailed deer fawns in coastal South Carolina. Journal of Fish and

    Wildlife Management 4:280-289.

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time of elk. Applied

    Animal Behaviour Science 29:251-267.

Michael, E. D. 1970. Activity patterns of white-tailed deer in south Texas. The Texas Journal of

    Science 21:417-428.

Moen, A. N. 1968. Energy exchange of white-tailed deer, western Minnesota. Ecology 49:676-

    682.

Moen, A. N. 1976. Energy conservation by white-tailed deer in the winter. Ecology 57:192-198.

Montague, D. M., R. D. Montague, M. L. Fies, and M. J. Kelly. 2017. Using distance-sampling

    to estimate density of white-tailed deer in forested, mountainous landscapes in Virginia.

    Northeastern Naturalist 24:505-519.

Montgomery, G. G. 1963. Nocturnal movements and activity rhythms of white-tailed deer.

    Journal of Wildlife Management 27:422-427.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. M. Conner. 2015. Coyote and

    bobcat predation on white-tailed deer fawns in a longleaf pine ecosystem in

southwestern Georgia. Journal of the Southeastern Association of Fish and Wildlife
Agencies 2:208-213.

North Carolina Climate Office. 2019. Wind Rose. <climate.ncsu.edu/windrose?state=SC&
station=KDYB>. Accessed 10 December 2019.

Ozoga, J. J. and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. Journal of
Wildlife Management 36:892-896.

Paige, K. N. 1995. Bats and barometric pressure: conserving limited energy and tracking insects
from the roost. Functional Ecology 9:463-467.

Parker, K. L. 1988. Effect of heat, cold, and rain on coastal black-tailed deer. Canadian Journal
of Zoology 66:2475-2483.

Pledger, J. M. 1975. Activity, home range, and habitat utilization of white-tailed deer,
Odocoileus virginianus, in southeastern Arkansas. Thesis, University of Arkansas,
Fayetteville, USA.

Prugh, L. R., and C. D. Golden. 2014. Does moonlight increase predation risk? Meta-analysis
reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal
Ecology 83:504-514.

Rogers, L. L., A. N. Moen, and M. L. Shedd. 1987. Rectal temperature of 2 free-ranging white-
tailed deer fawns. Journal of Wildlife Management 51:59-62.

Ruzicka, R. E., and M. R. Conover. 2012. Does weather or site characteristics influence the
ability of scavengers to locate food? Ethology 118:187-196.

Simoneaux, T. N. 2015. Space-use and movements of adult male white-tailed deer in
northeastern Louisiana. Thesis, University of Georgia, Athens, Georgia USA.

Sauer, P. R. 1984. Physical Characteristics. Pages 73-90 in L. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-215.

Sherfy, M. H., and P. J. Pekins. 1995. Influence of wind speed on sage grouse metabolism. Canadian Journal of Zoology 73:749-754.

Stander, P. E. 1992. Foraging dynamics of lions in a semi-arid environment. Canadian Journal of Zoology 70:8-21.

Sullivan, J. D., S. S. Ditchkoff, B. A. Collier, C. R. Ruth, and J. B. Raglin. 2016. Movement with the moon: white-tailed deer activity and solunar events. Journal of the Southeastern Association of Fish and Wildlife Agencies 3:225-232.

Tilton, M. E., and E. E. Willard. 1982. Winter habitat selection in mountain sheep. Journal of Wildlife Management. 46:359-366.

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

Valix, M., H. Fritz, A. J. Loveridge, Z. Davidson, J. E. Hill, F. Murindagomo, and D. W. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behavior at waterholes? Behavioral Ecology and Sociobiology 63:1483-1494.

von Bartheld, C. S., and F. Giannessi. 2011. The paratympanic organ: a barometer and altimeter in the middle ear of birds? Journal of Experimental0 Zoology B Molecular and Developmental Evolution 316:402-408.

Webb, S. L., C. V. Olson, M. R. Dzialak, S. M. Harju, J. B. Winstead, and D. Lockman. 2012. Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. Ecological Processes 1:2-15.

Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. DeYoung. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology 2010:1-12.

Weber, A. H., and J. O. Blanton. 1980. Monthly mean wind fields for the South Atlantic Bight. Journal of Physical Oceanography 10:1256-1263.

Wells, M.C. 1978. Coyote senses in predation: environmental influences on their relative use. Behavioural Processes 3:149-158.

Wells, M. C., and P. N., Lehner. 1978. The relative importance of the distance senses in coyote predatory behavior. Animal Behaviour 26:251-258.

Wiskirchen, K. H. 2017. Survival of adult white-tailed deer and movement relative to temporal patterns of predation risk. Thesis, Auburn University, Auburn, Alabama, USA.

Zagata, M. D., and A. O. Haugen. 1974. Influence of light and weather on observability of Iowa deer. Journal of Wildlife Management 38:220-228.

Table 2.1. Candidate models, degrees of freedom (df), Akaike's Information Criterion (AIC$_c$), and associated model ranks (ΔAIC$_c$) and model weights (w$_i$) used to predict periods of peak white-tailed deer activity surrounding sunrise and sunset at Brosnan Forest, South Carolina.

Crepuscular Period Duration							
Sunrise Period		Sunset Period					
Hours Before	Hours After	Hours Before	Hours After	df	AICc	Δ AICc	wi
1.5	1.5	1.5	1.5	5	550490.6	0.00	1.00
1.0	1.0	1.5	1.5	5	551043.1	552.55	0.00
1.5	1.5	2.0	2.0	5	551921.4	1430.83	0.00
1.0	1.0	2.0	2.0	5	552748.2	2257.63	0.00
2.0	2.0	1.5	1.5	5	553181.9	2691.37	0.00
1.5	1.5	1.0	1.0	5	554075.2	3584.65	0.00
1.0	1.0	1.0	1.0	5	554262.5	3771.97	0.00
2.0	2.0	2.0	2.0	5	554473.0	3982.41	0.00
2.0	2.0	1.0	1.0	5	556923.9	6433.37	0.00
N/A	N/A	N/A	N/A	2	625594.3	75103.72	0.00

Table 2.2. Candidate models, degrees of freedom (df), Akaike's Information Criterion (AIC$_c$), and associated model ranks (ΔAIC$_c$) and model weights (w$_i$) used to predict periods of white-tailed deer activity using different metrics of barometric pressure at Brosnan Forest, South Carolina.

Model	df	AIC$_c$	ΔAIC$_c$	w$_i$
4-hour rate	195	539557.2	0.00	1.00
Current barometric pressure	200	540697.8	1140.54	0.00
24-hour rate	188	540731.1	1173.82	0.00
Null	128	541503.5	1946.28	0.00
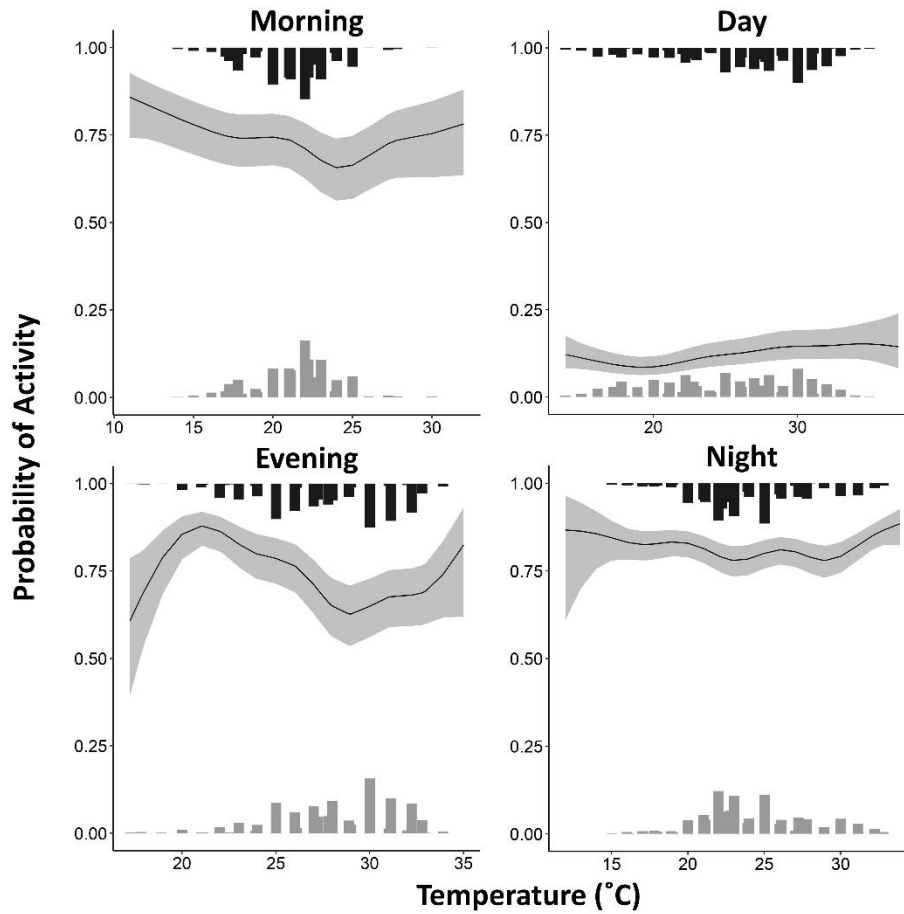
Figure 2.1. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult males during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
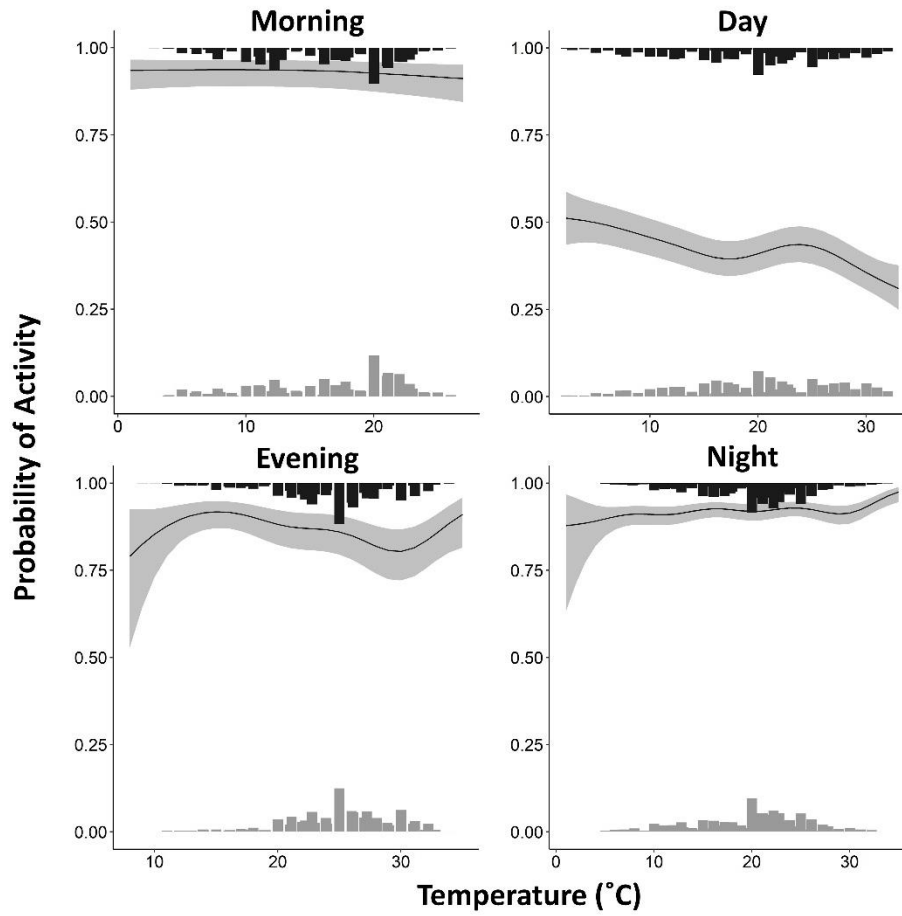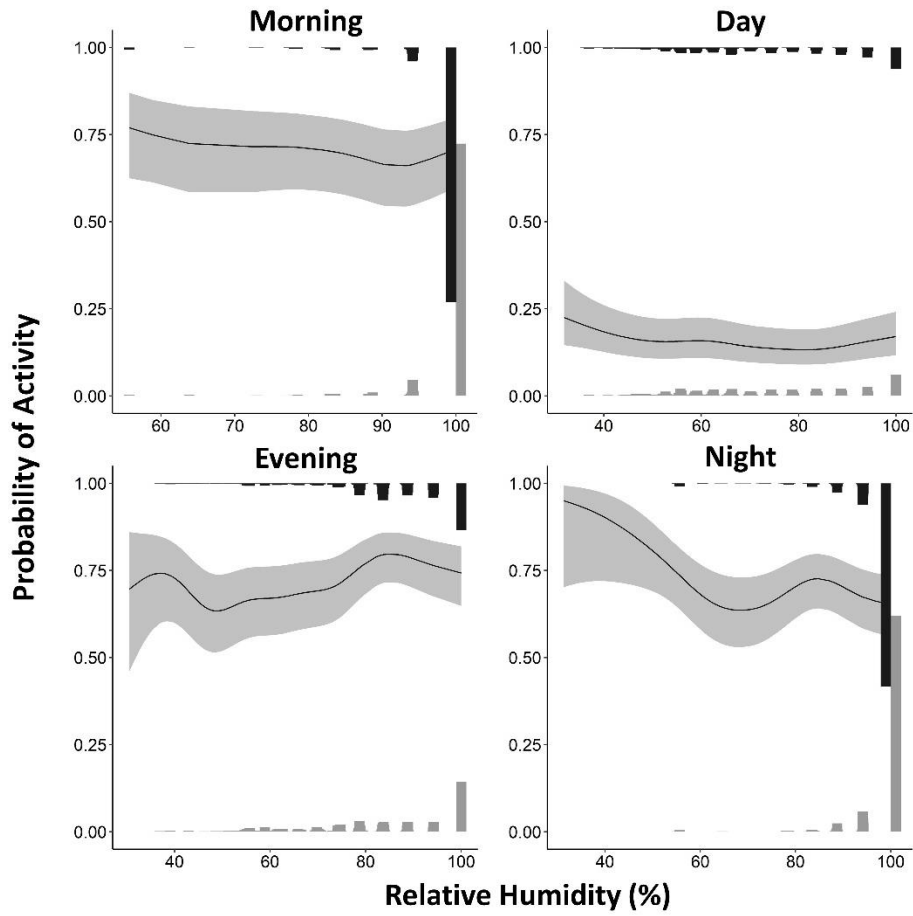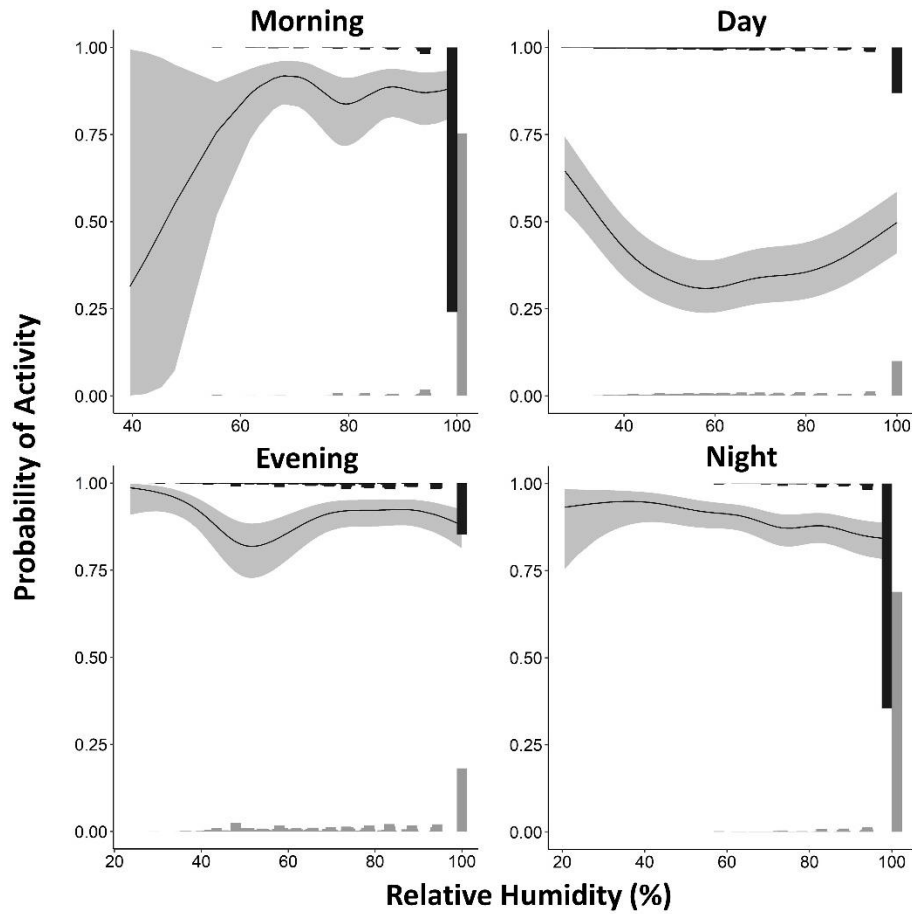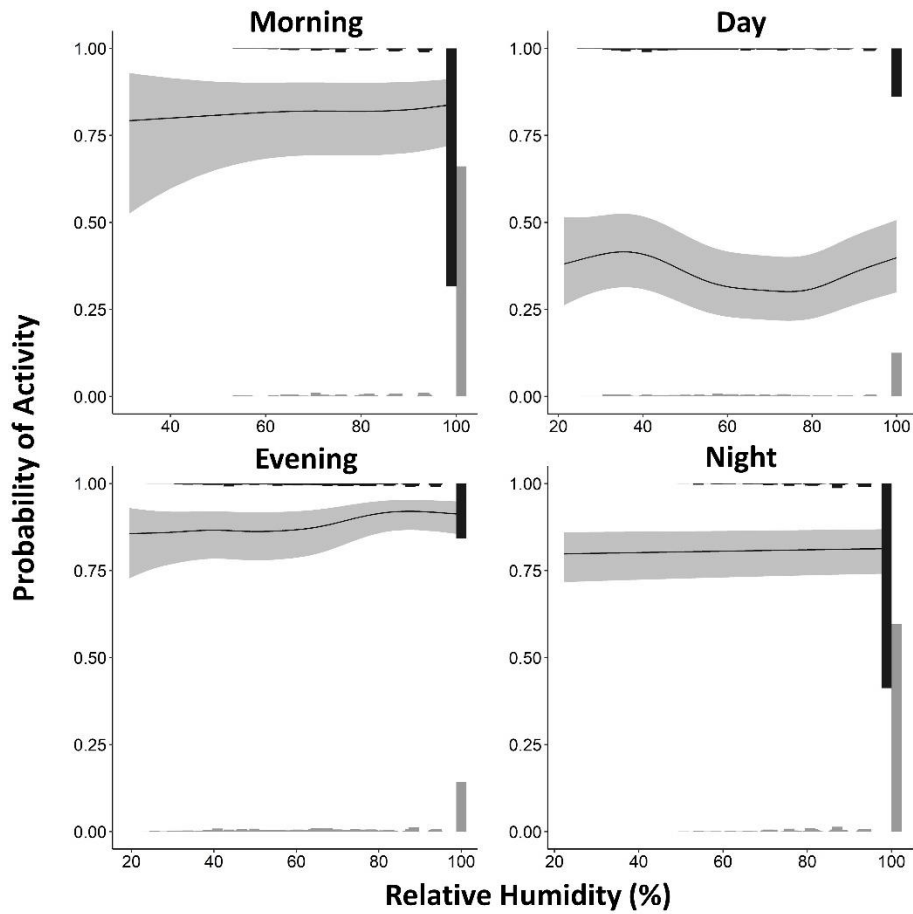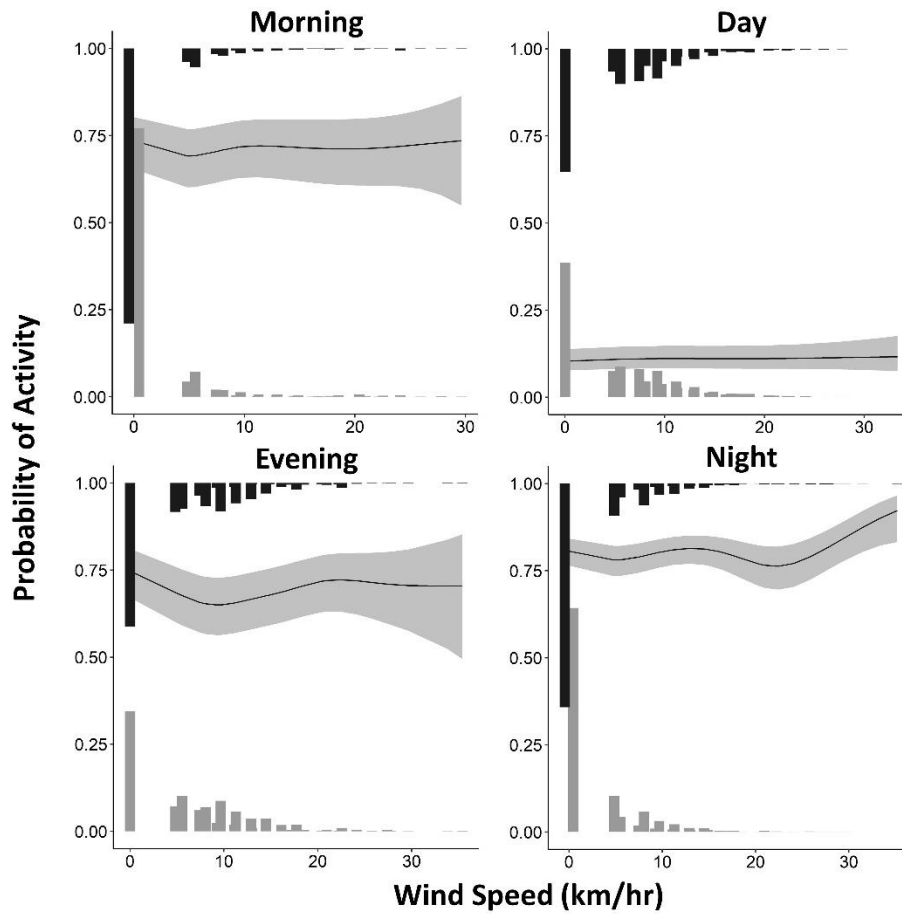
Figure 2.2. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult males during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
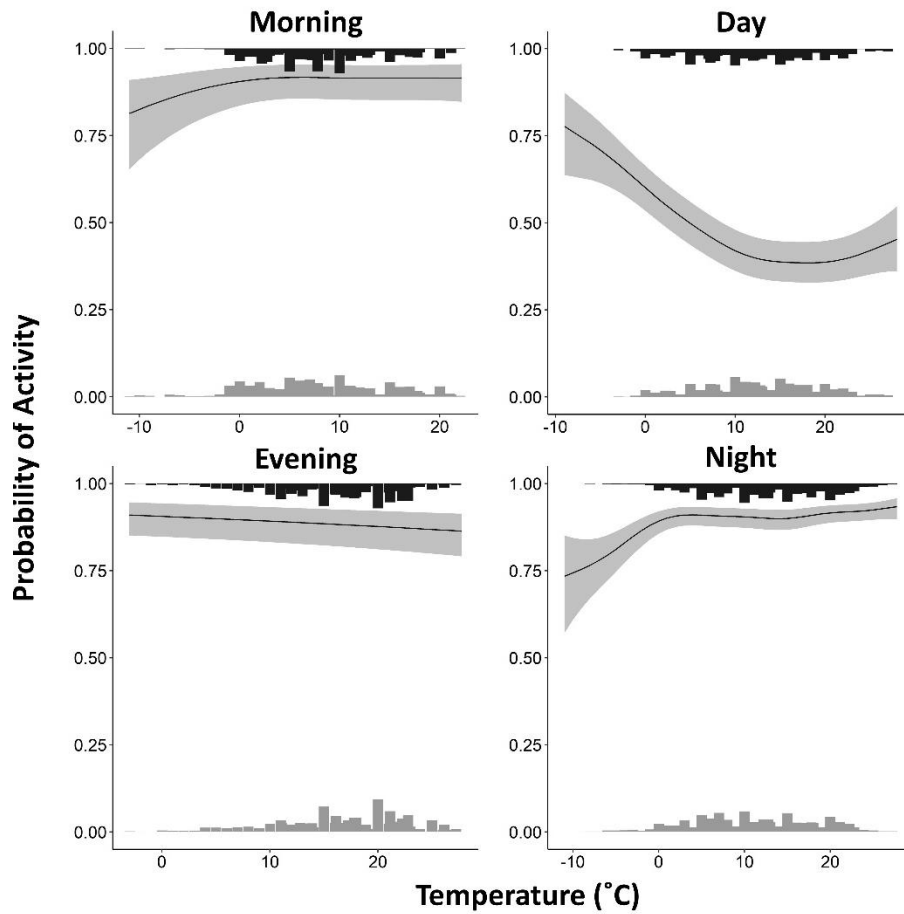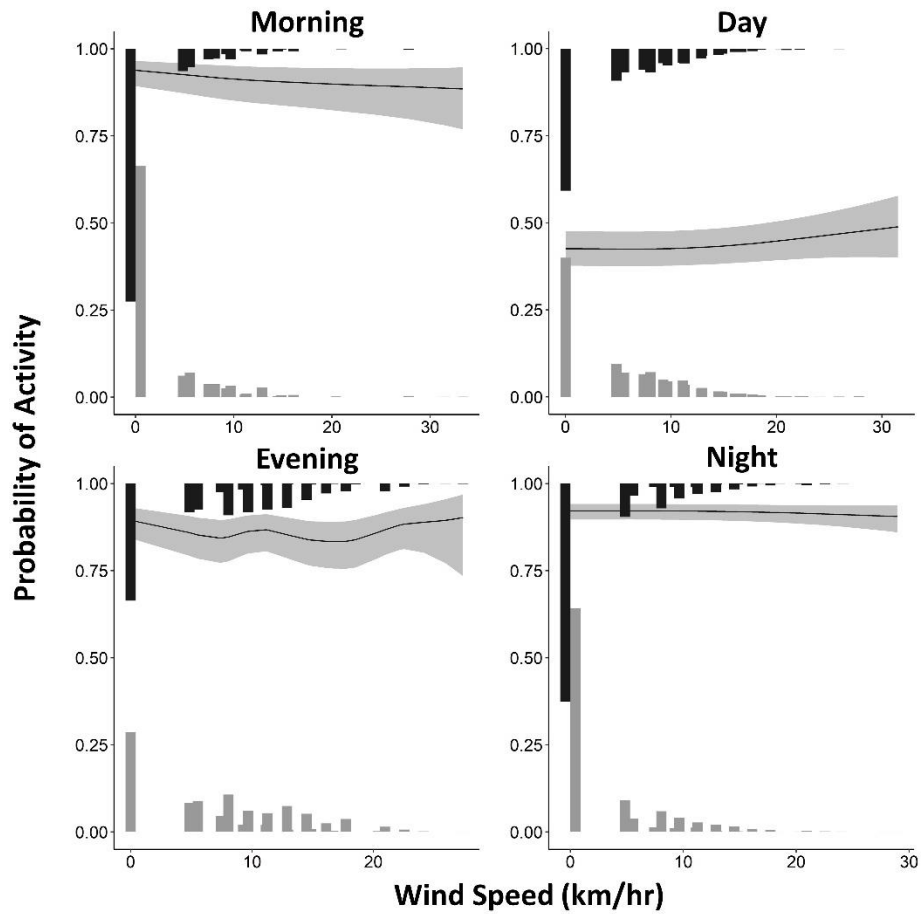
Figure 2.3. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult males during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
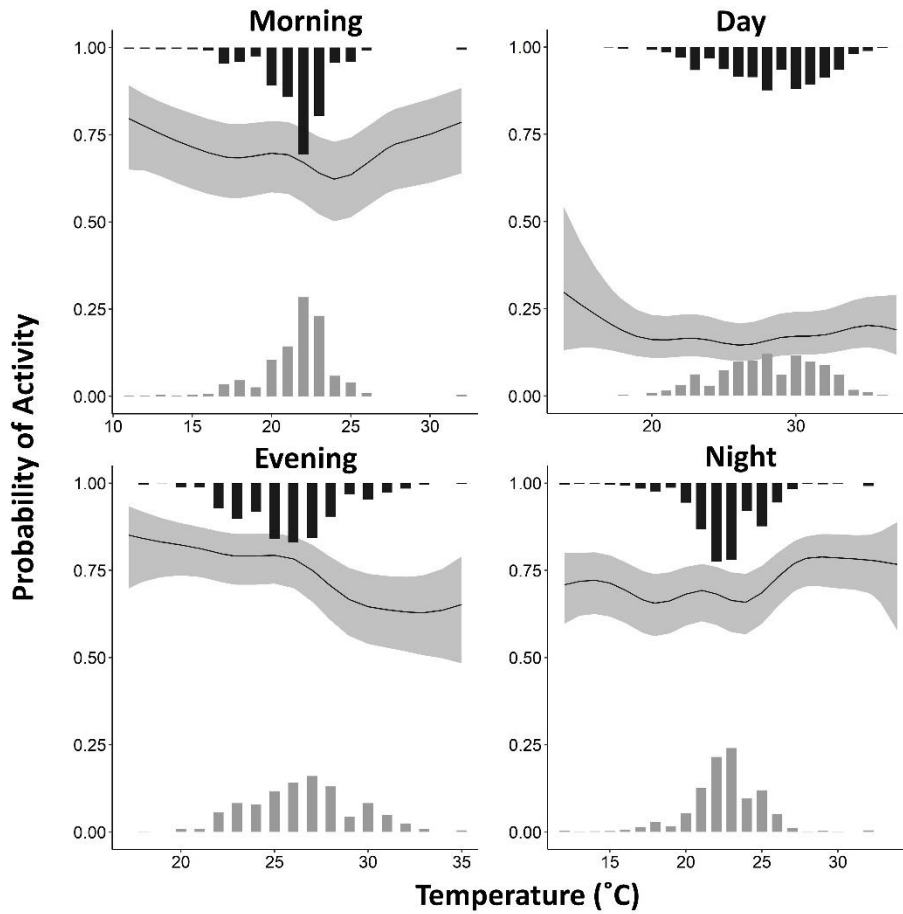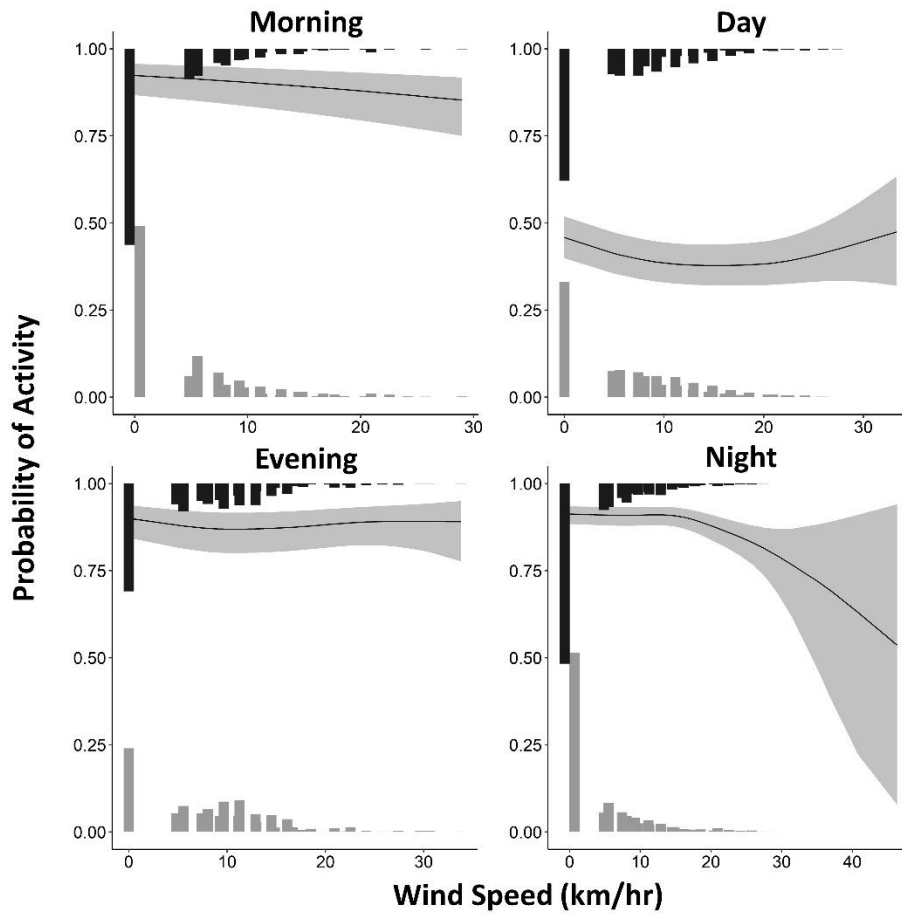
Figure 2.4. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult females during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
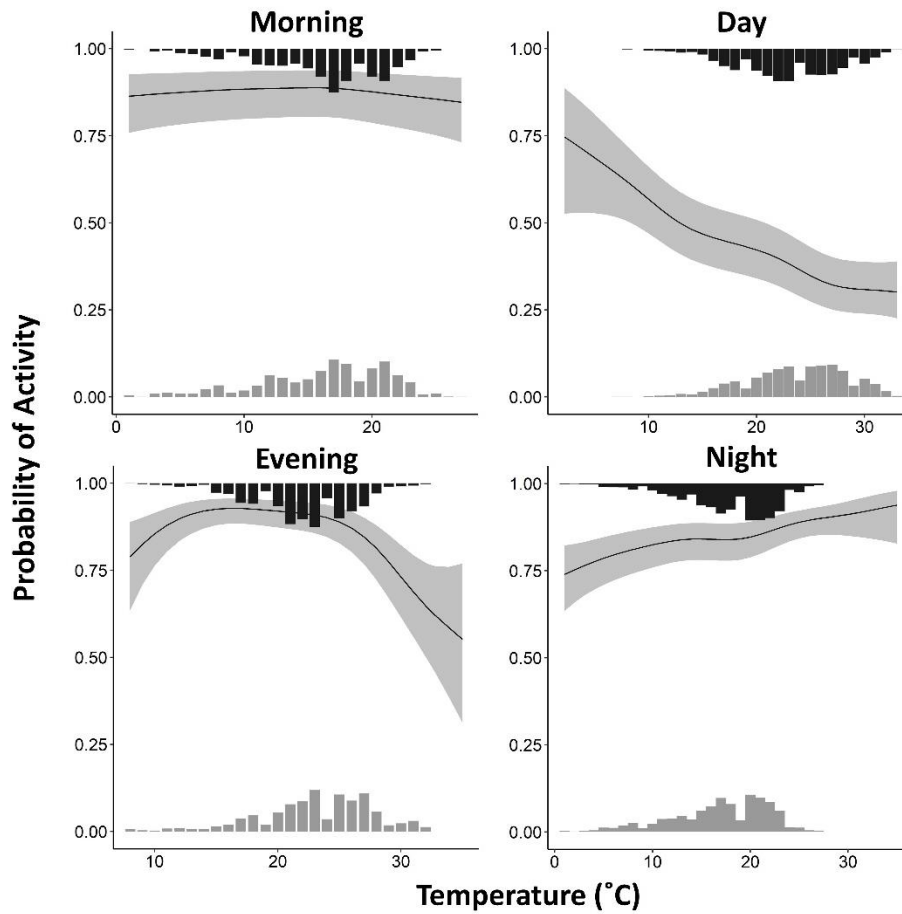
Figure 2.5. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult females during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
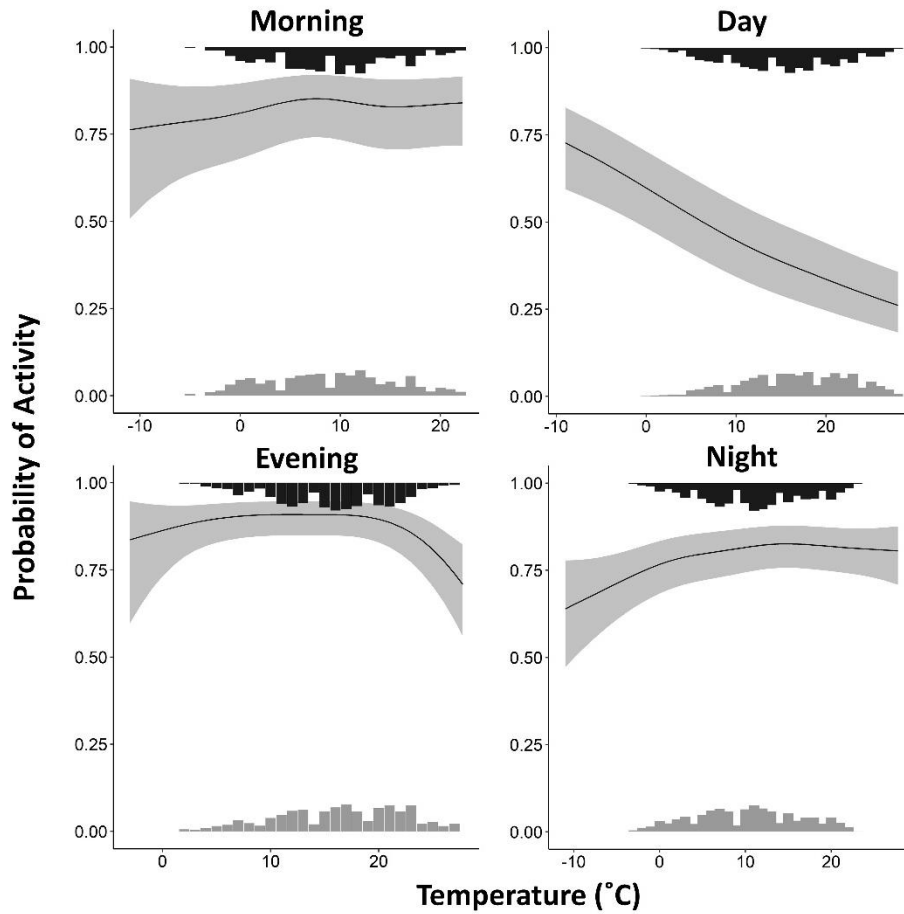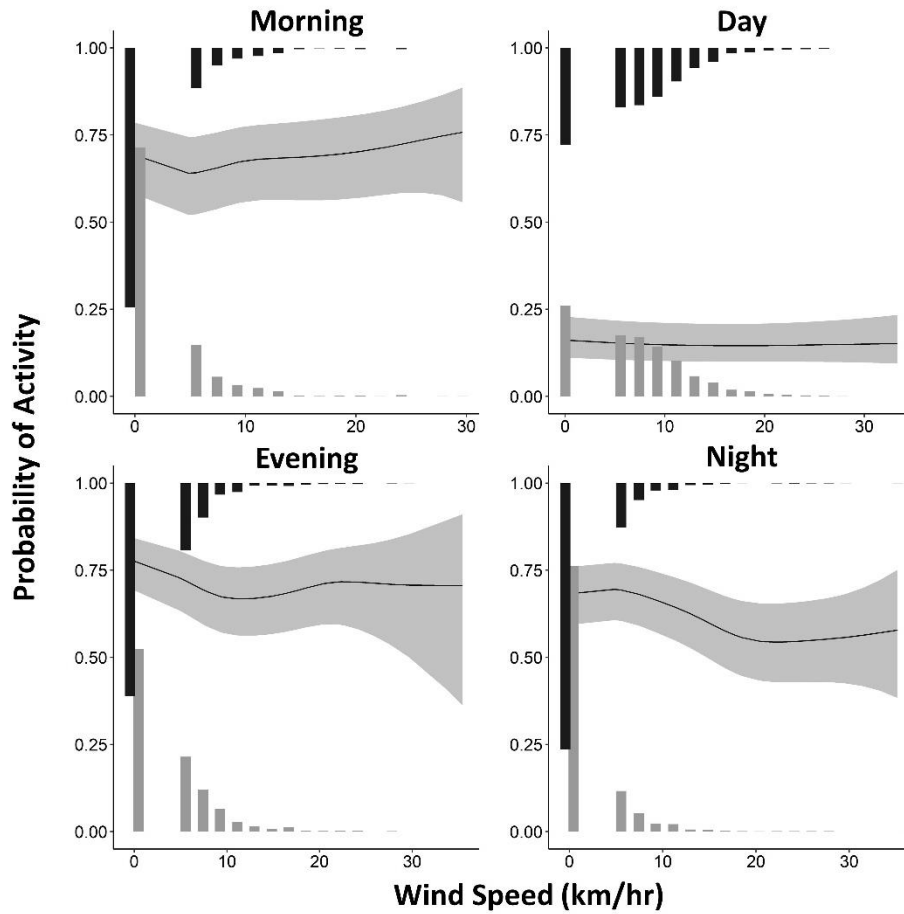
Figure 2.6. Model estimated average probability of activity (95% CL) relative to time of day and ambient temperature for adult females during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the temperature data used to inform the model.
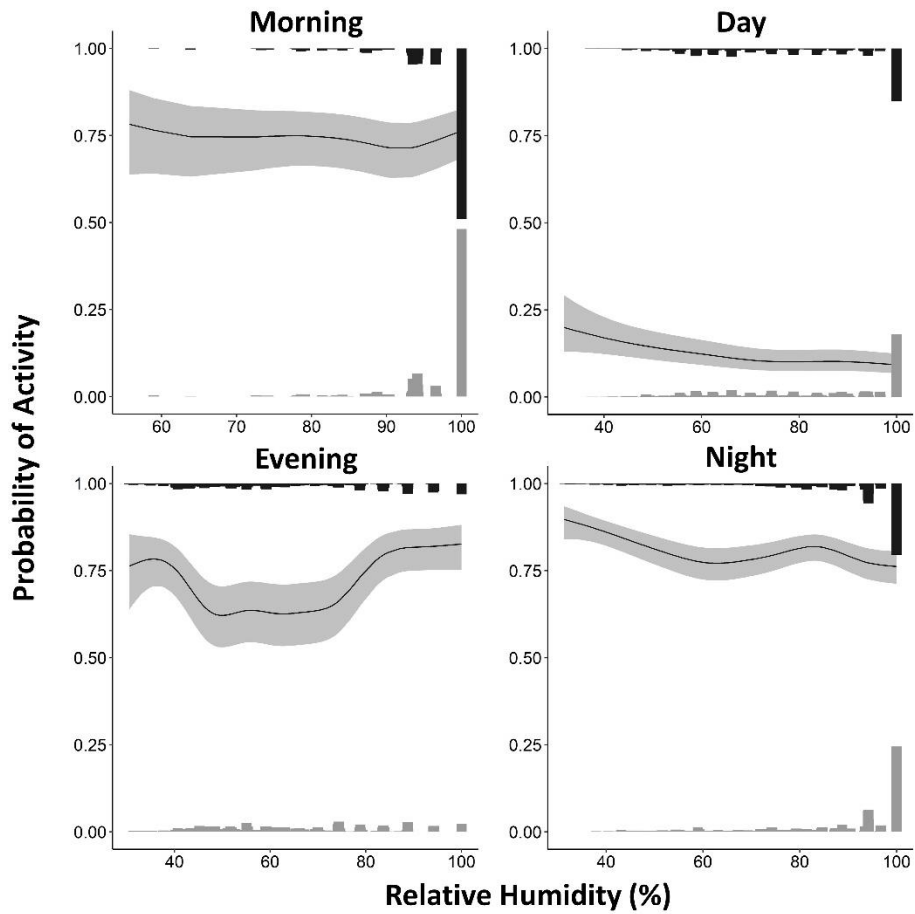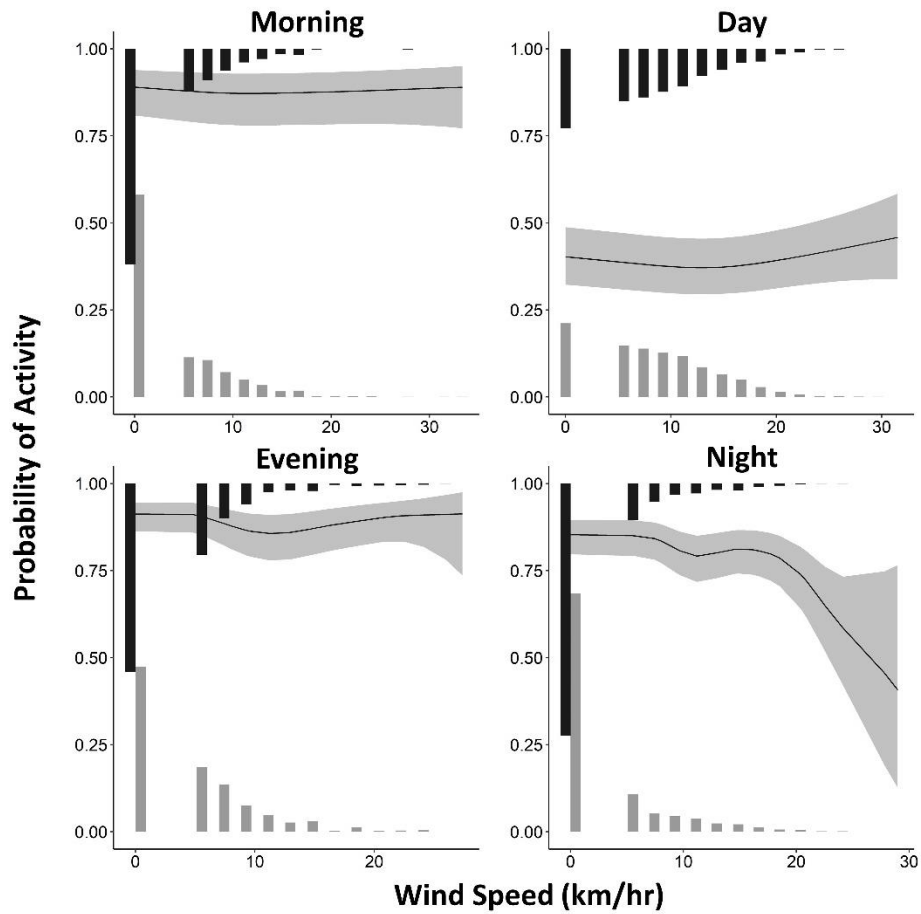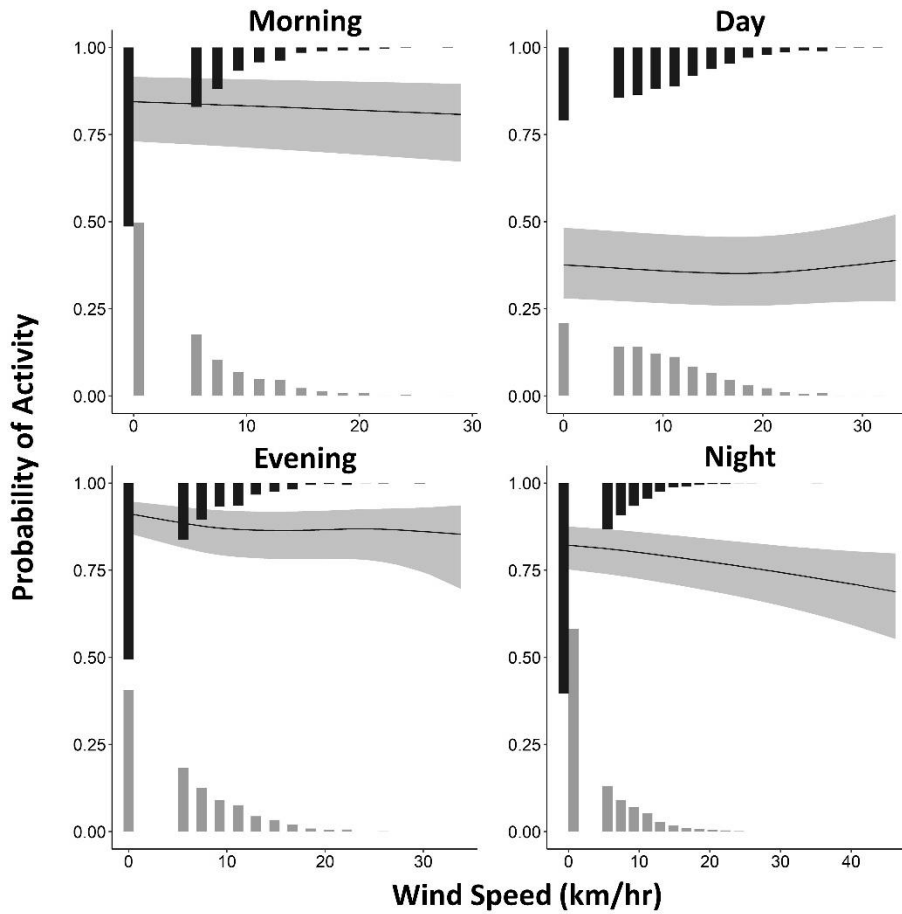
Figure 2.7. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult males during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.
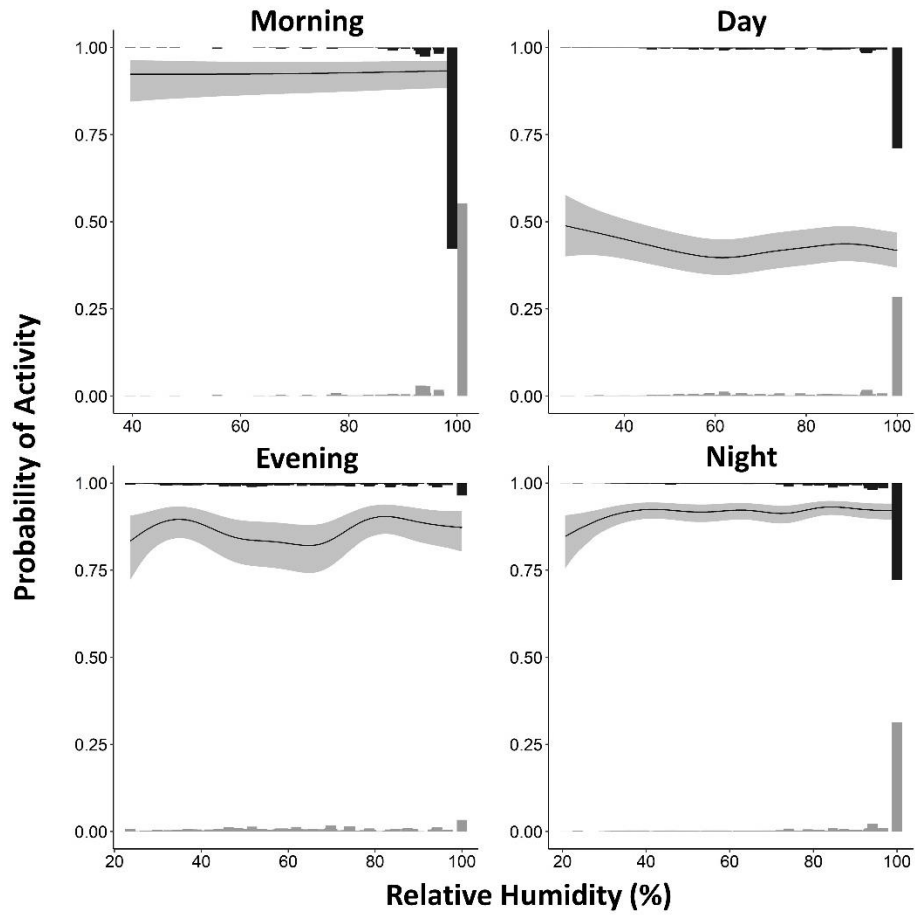
Figure 2.8. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult males during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.
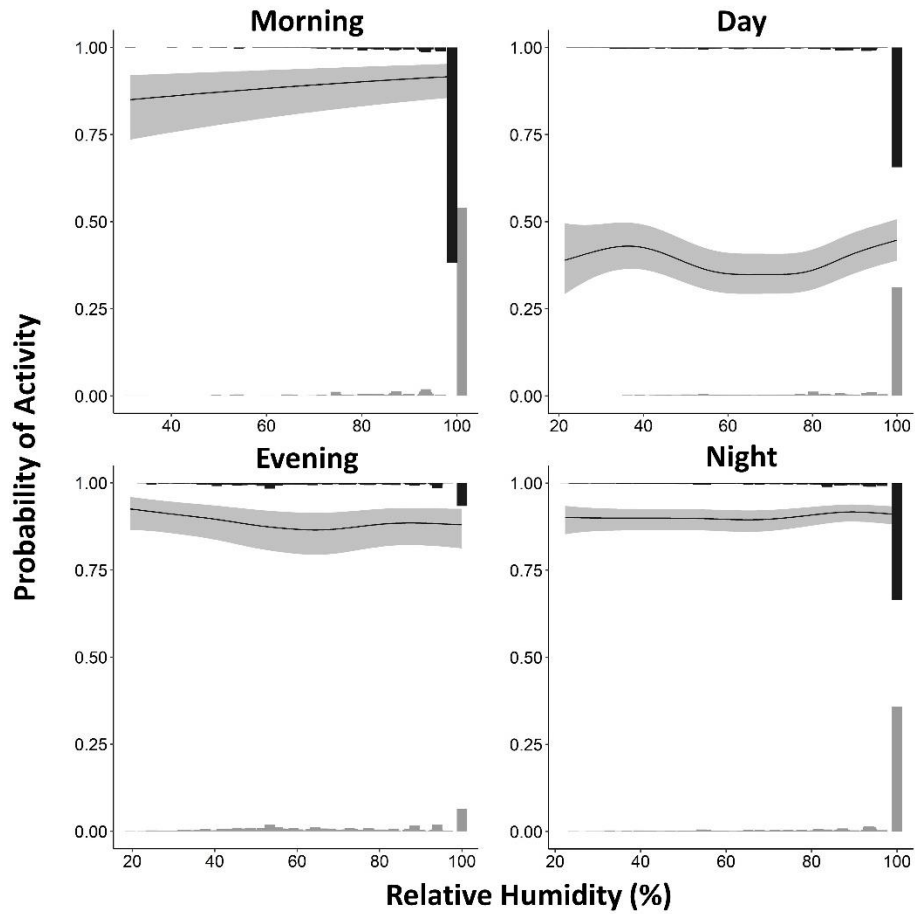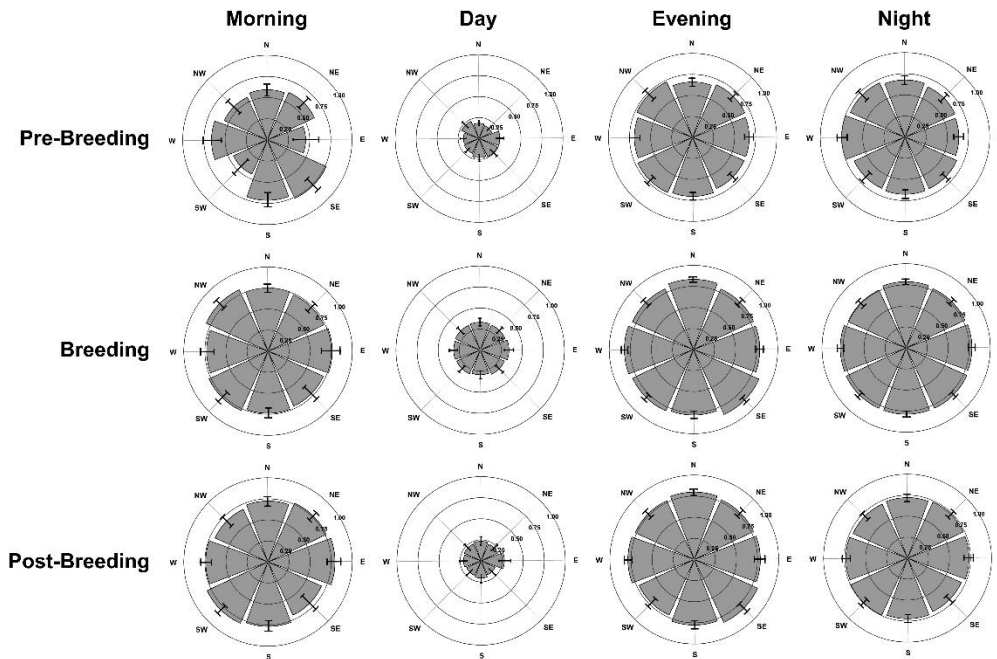
Figure 2.9. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult males during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.

Figure 2.10. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult females during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.

Figure 2.11. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult females during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.

Figure 2.12. Model estimated average probability of activity (95% CL) relative to time of day and relative humidity for adult females during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the relative humidity data used to inform the model.

Figure 2.13. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult males during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.
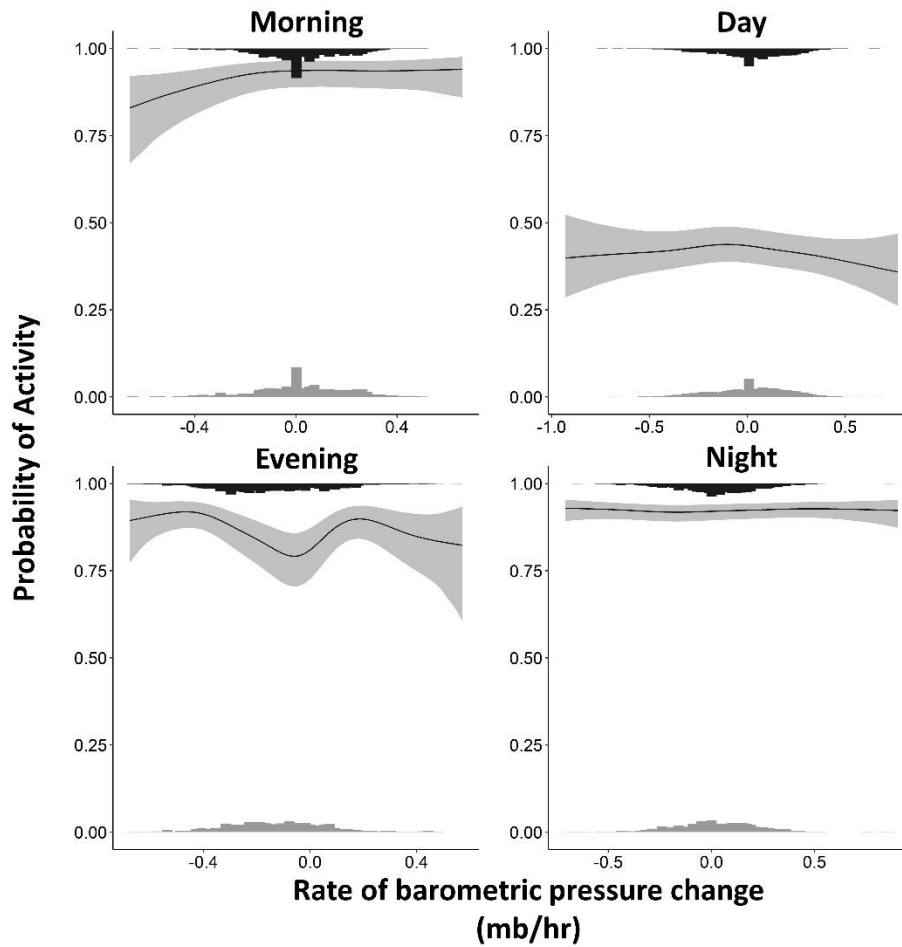
Figure 2.14. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult males during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.
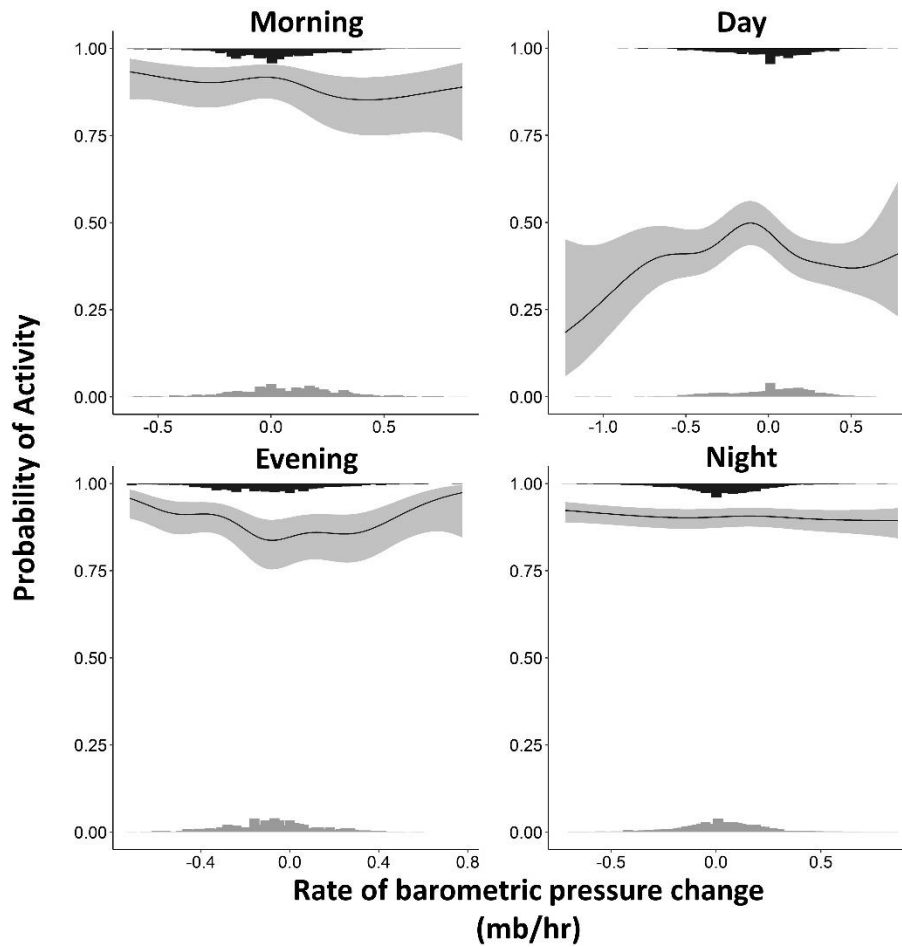
Figure 2.15. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult males during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.

Figure 2.16. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult females during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.
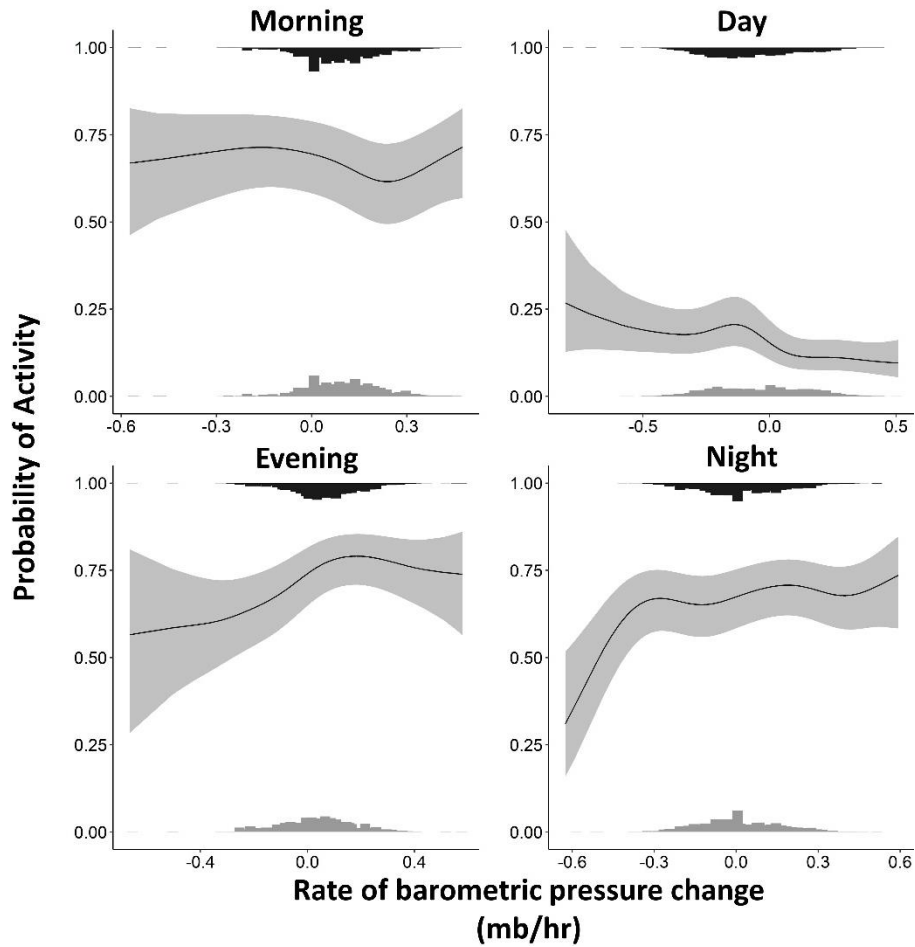
Figure 2.17. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult females during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.
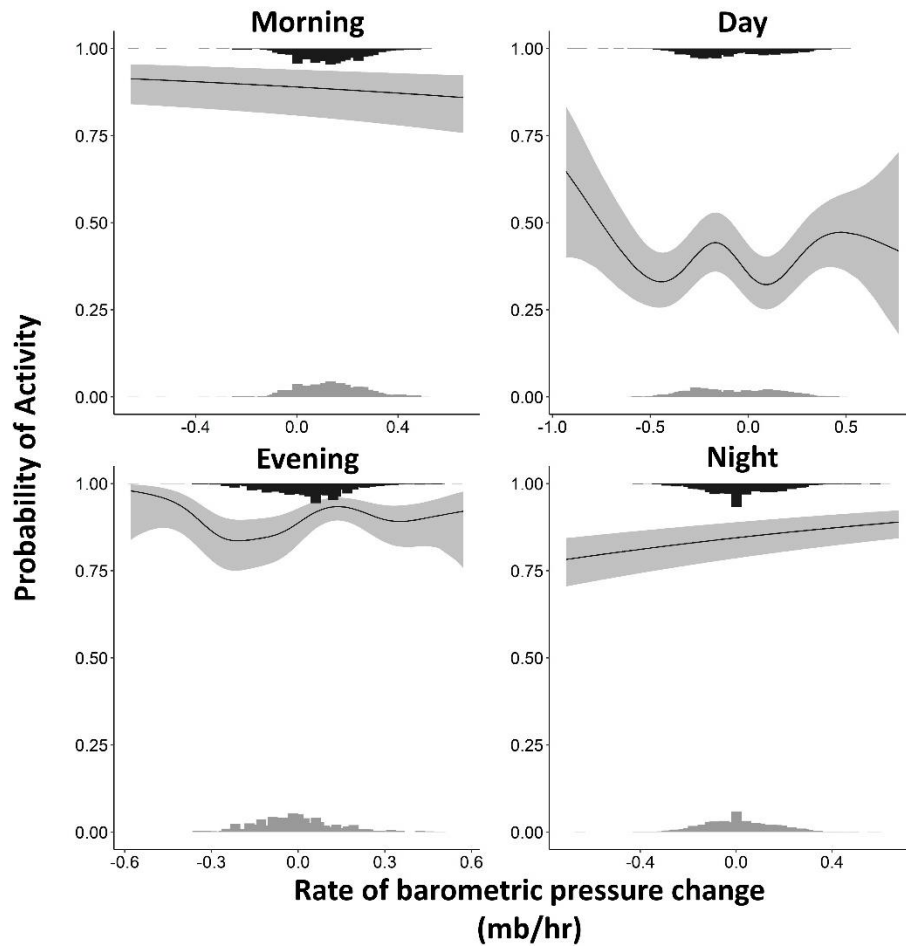
Figure 2.18. Model estimated average probability of activity (95% CL) relative to time of day and wind speed for adult females during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the wind speed data used to inform the model.
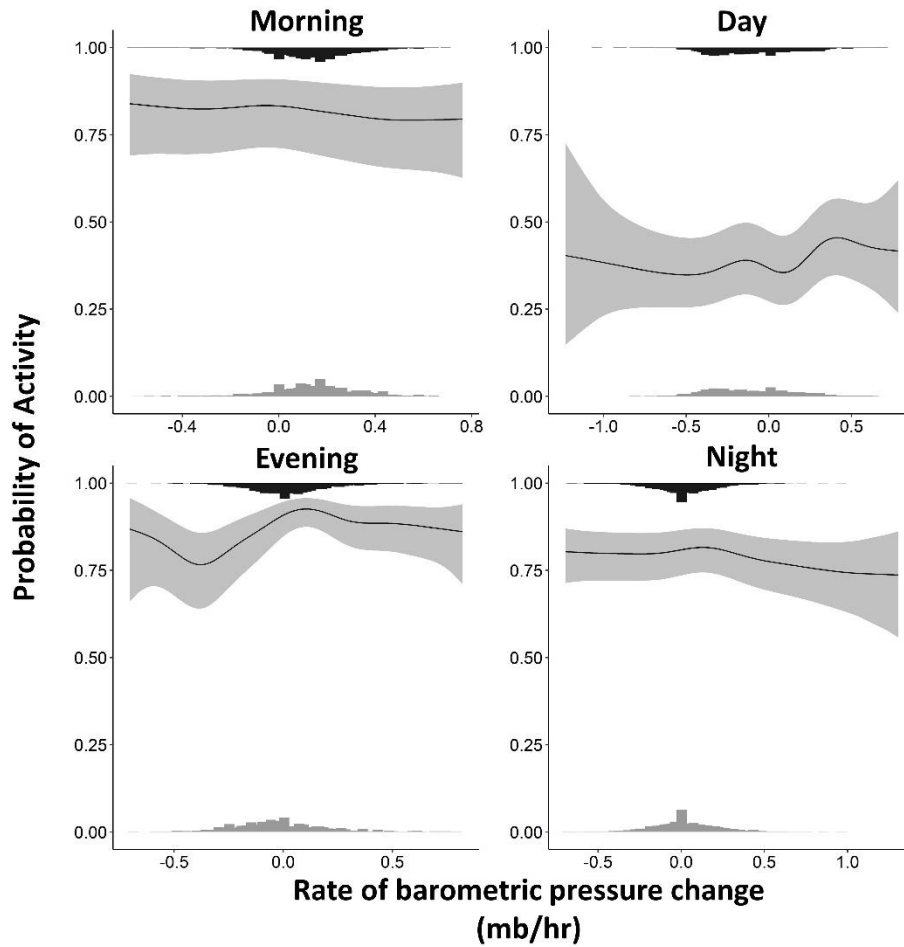
Figure 2.19. Model estimated probability of activity during any given 30-min interval for adult male white-tailed deer relative to wind direction during four periods of day (morning, day, evening, and night) within three seasons (pre-breeding, breeding, and post-breeding) in South Carolina.
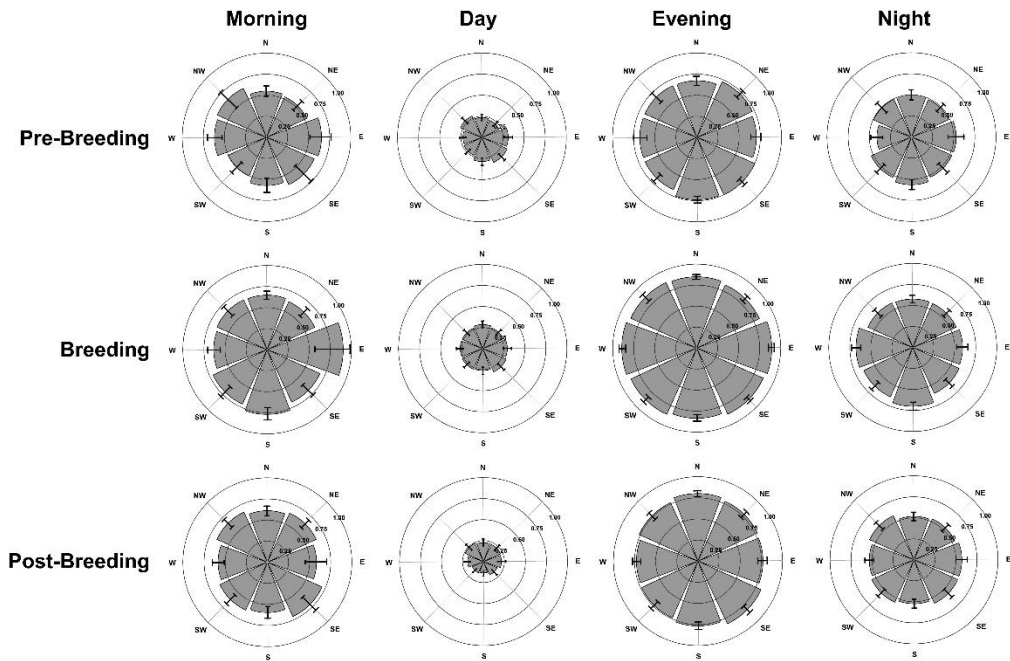
Figure 2.20. Model estimated probability of activity during any given 30-min interval for adult female white-tailed deer relative to wind direction during four periods of day (morning, day, evening, and night) within three seasons (pre-breeding, breeding, and post-breeding) in South Carolina.
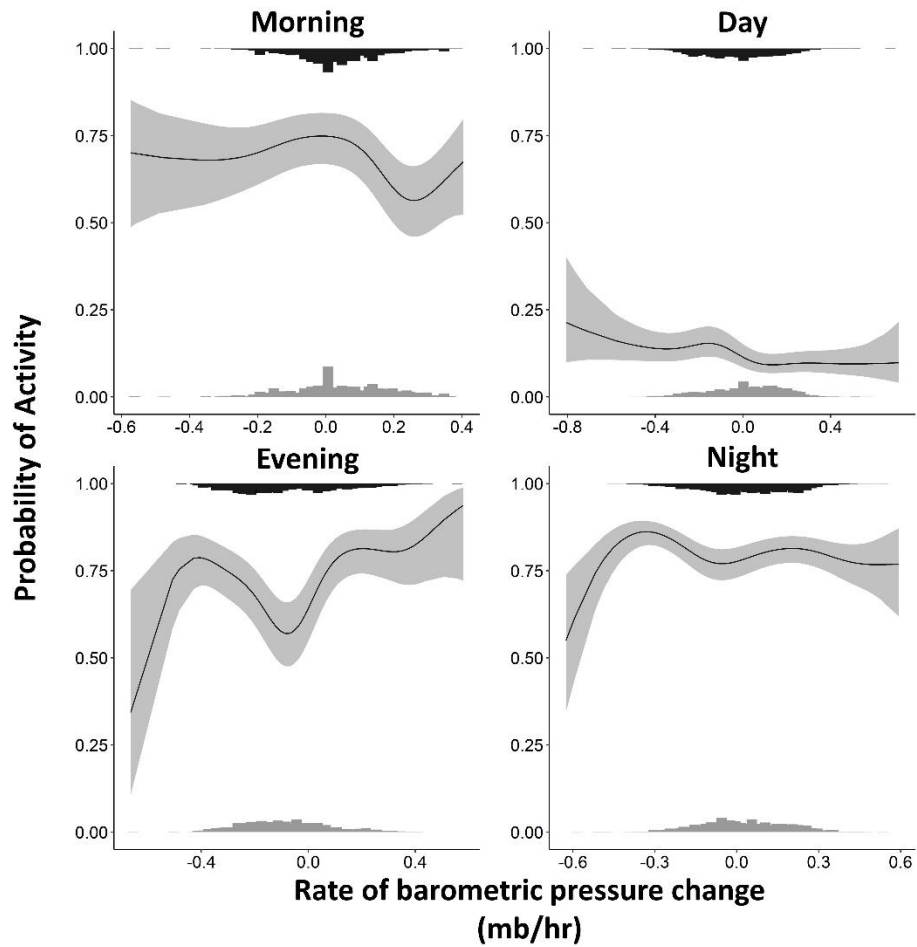
Figure 2.21. Model estimated average probability of activity (95% CL) relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.
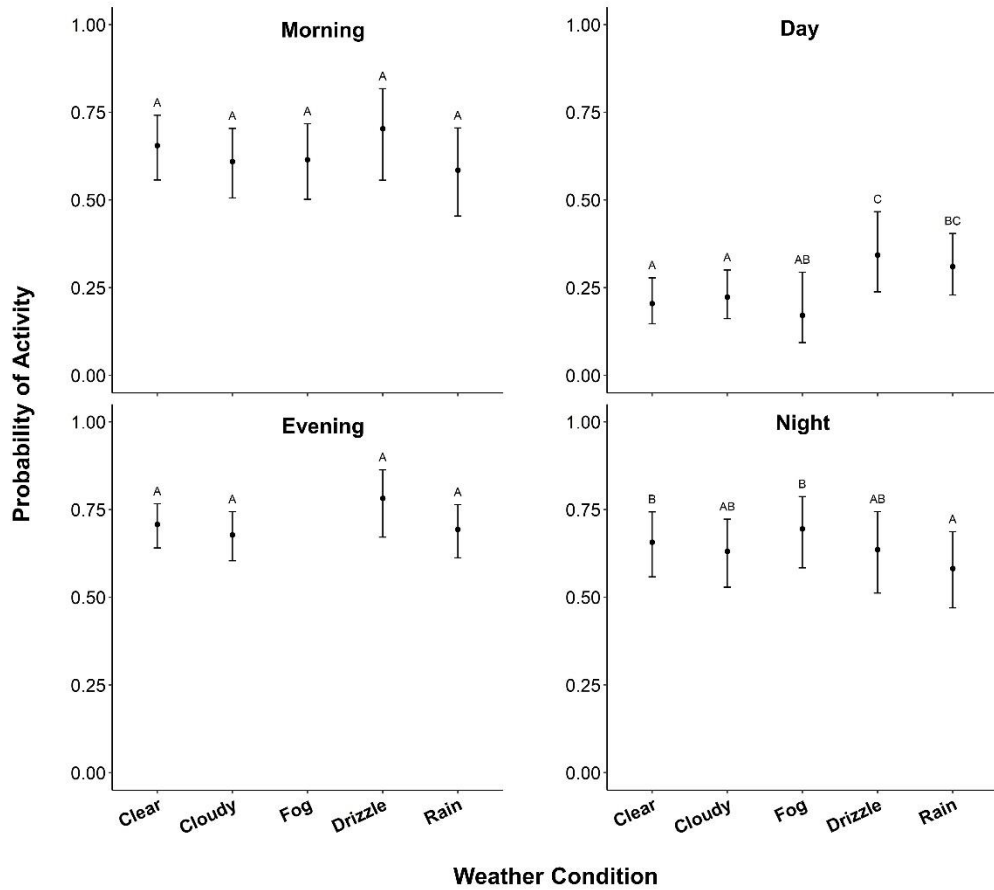
Figure 2.22. Model estimated average probability of activity (95% CL) relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.

Figure 2.23. Model estimated average probability of activity (95% CL) relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.

Figure 2.24. Model estimated average probability of activity (95% CL relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the pre-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.

Figure 2.25. Model estimated average probability of activity (95% CL) relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.

Figure 2.26. Model estimated average probability of activity (95% CL) relative to time of day and the hourly rate of change in barometric pressure over the previous 4 hours for adult males during the post-breeding season. Histograms on top (active fixes) and bottom (inactive fixes) of each plot represent distribution of the data used to inform the model.
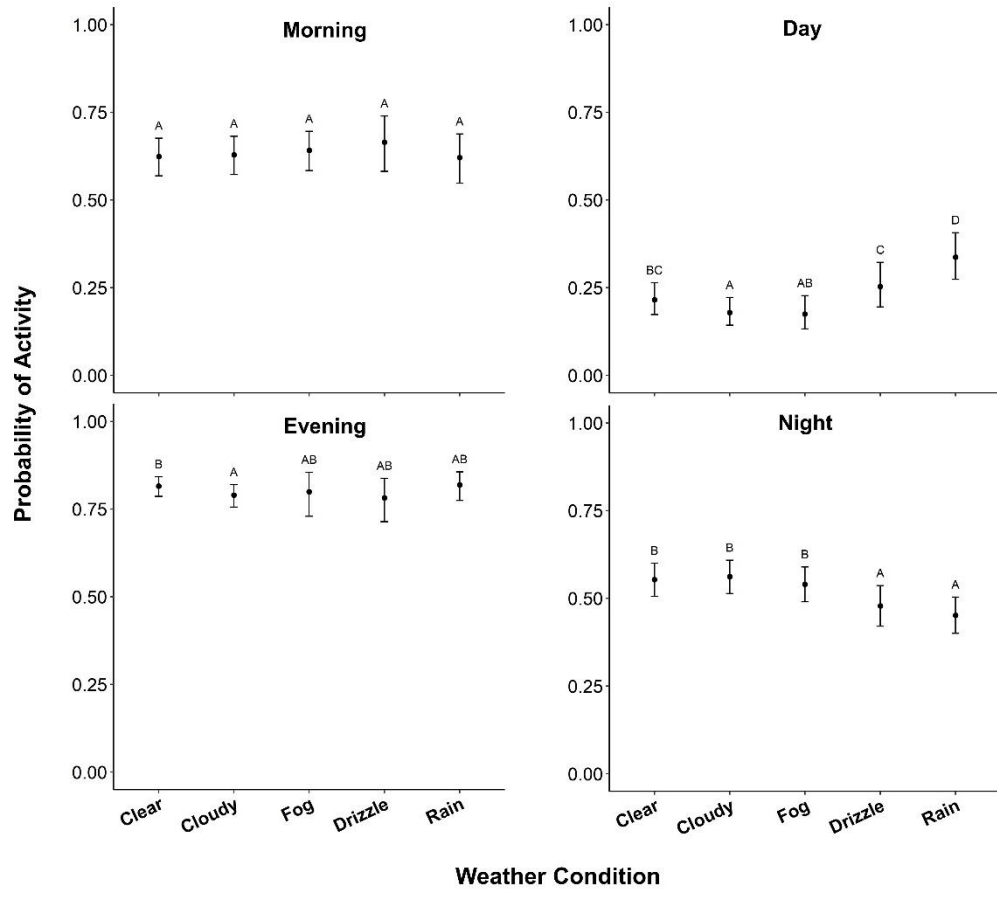
Figure 2.27. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult males during the pre-breeding season (letters indicate statistical significance at α=0.05). Fog was removed from analyses during the evening due to small sample size.
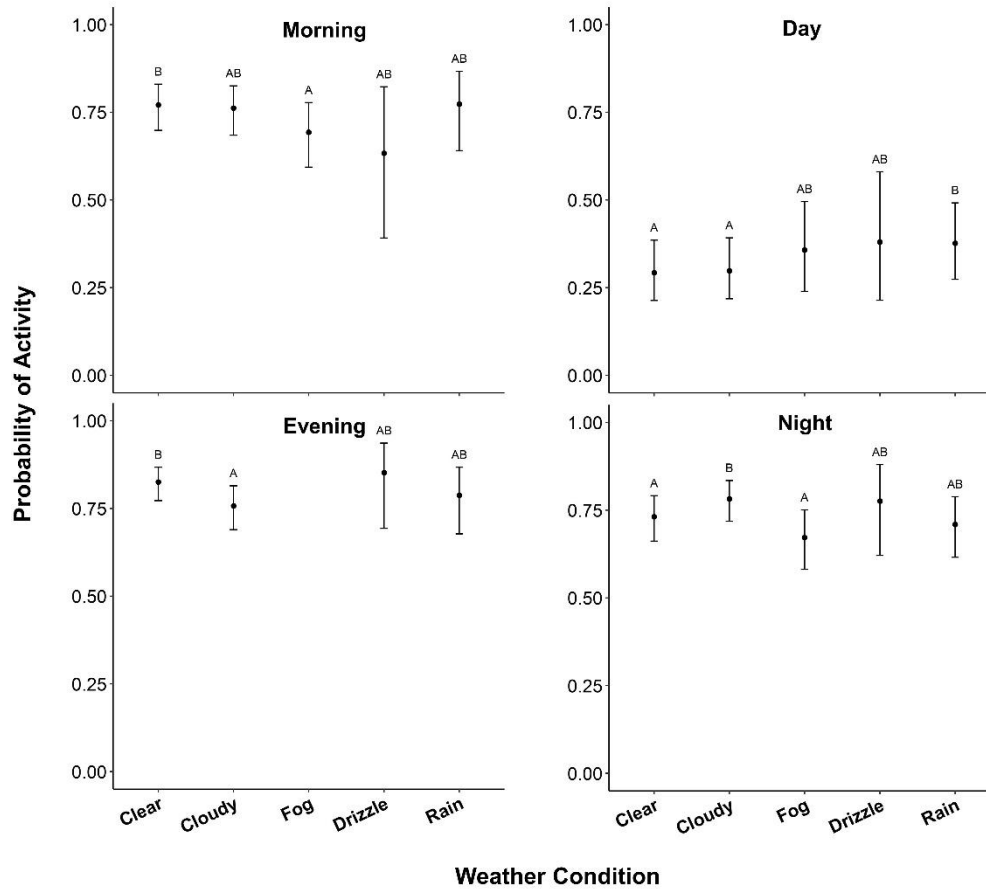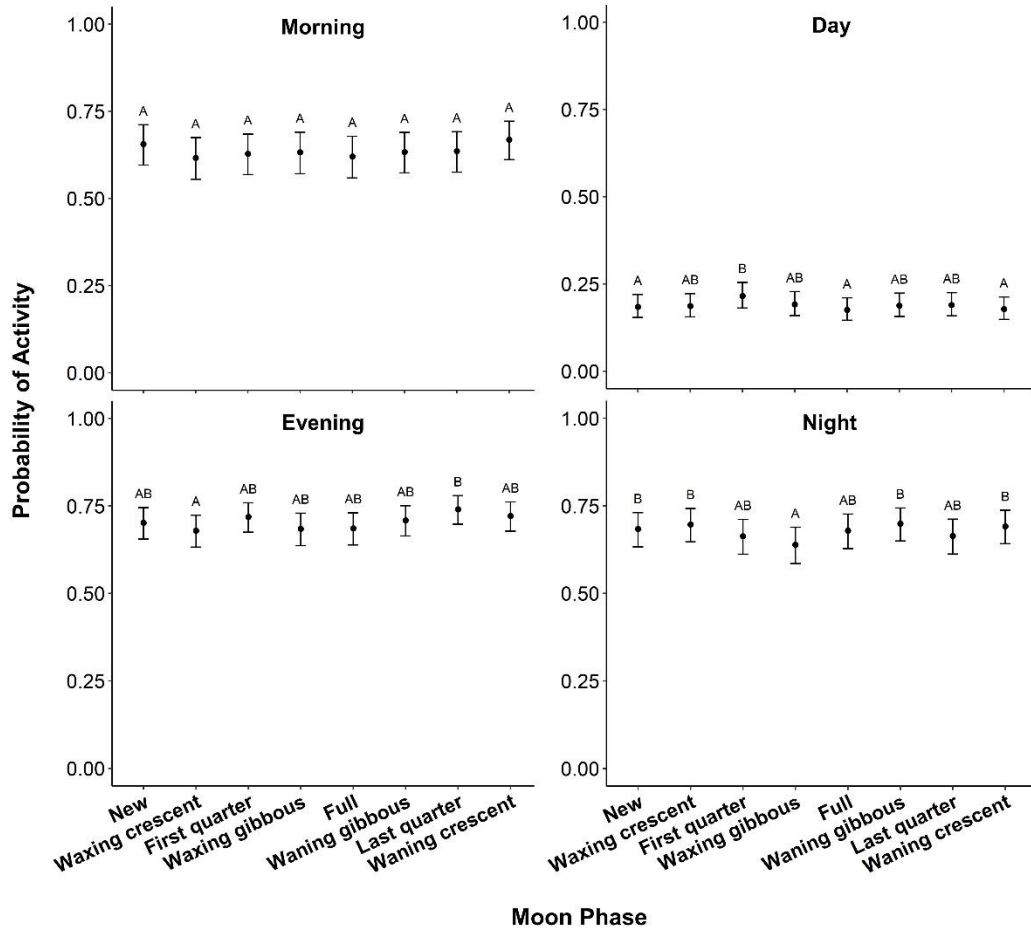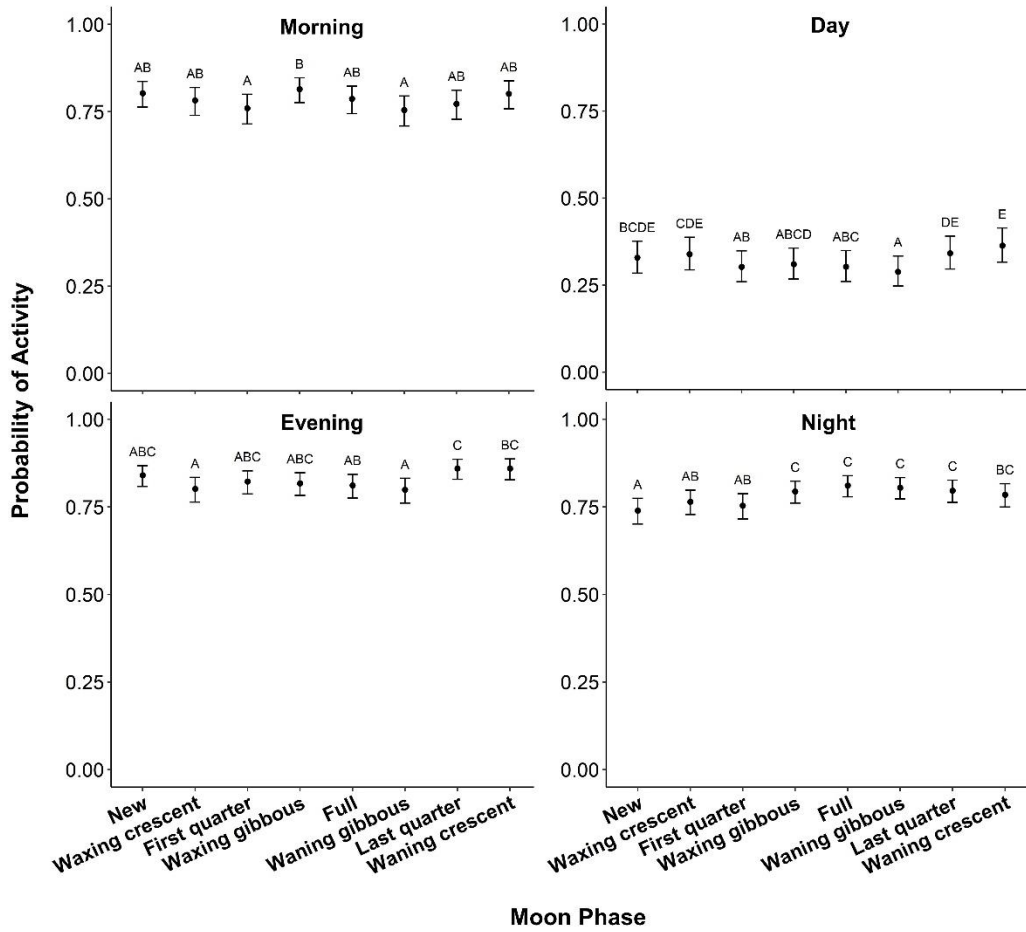
Figure 2.28. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult males during the breeding season (letters indicate statistical significance at α=0.05). Fog was removed from analyses during the evening due to small sample size.
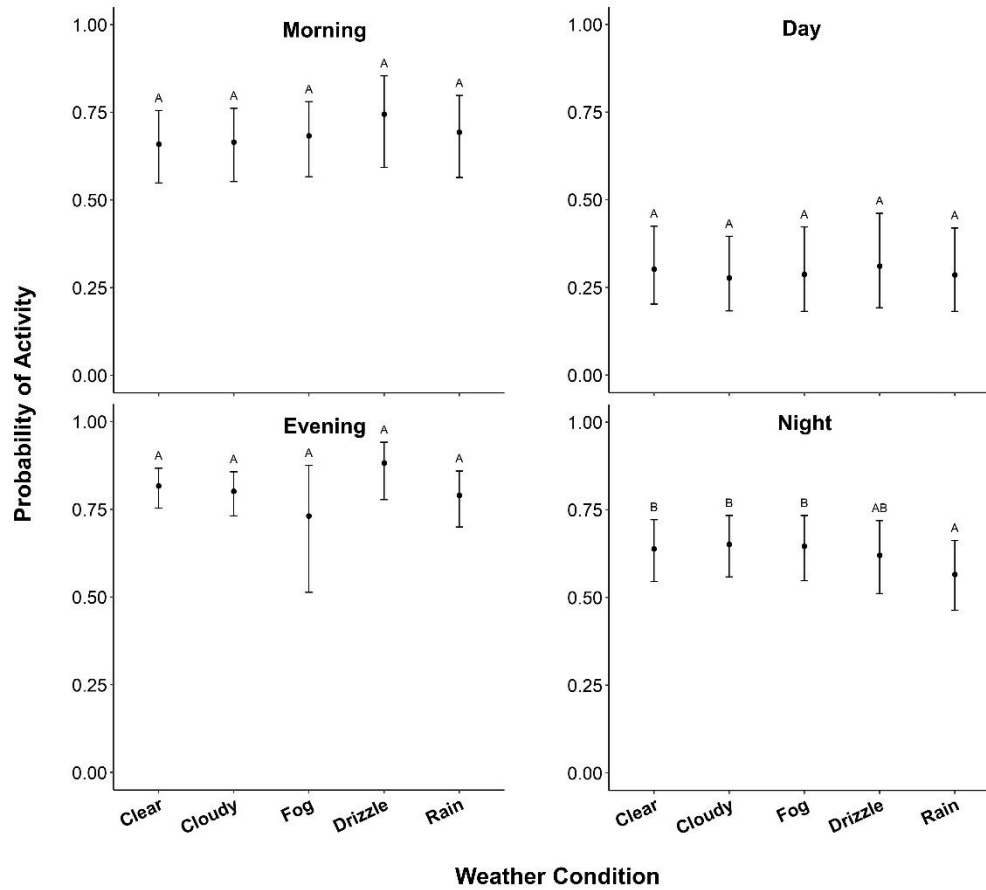
Figure 2.29. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult males during the post-breeding season (letters indicate statistical significance at α=0.05).
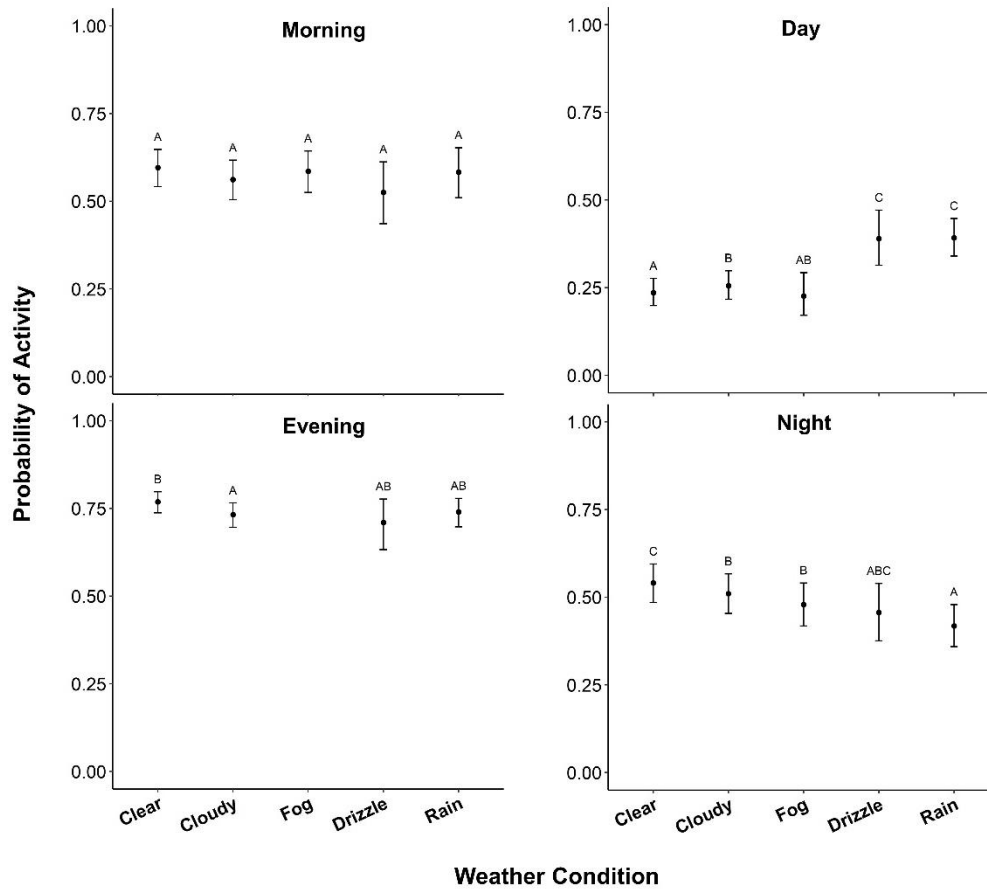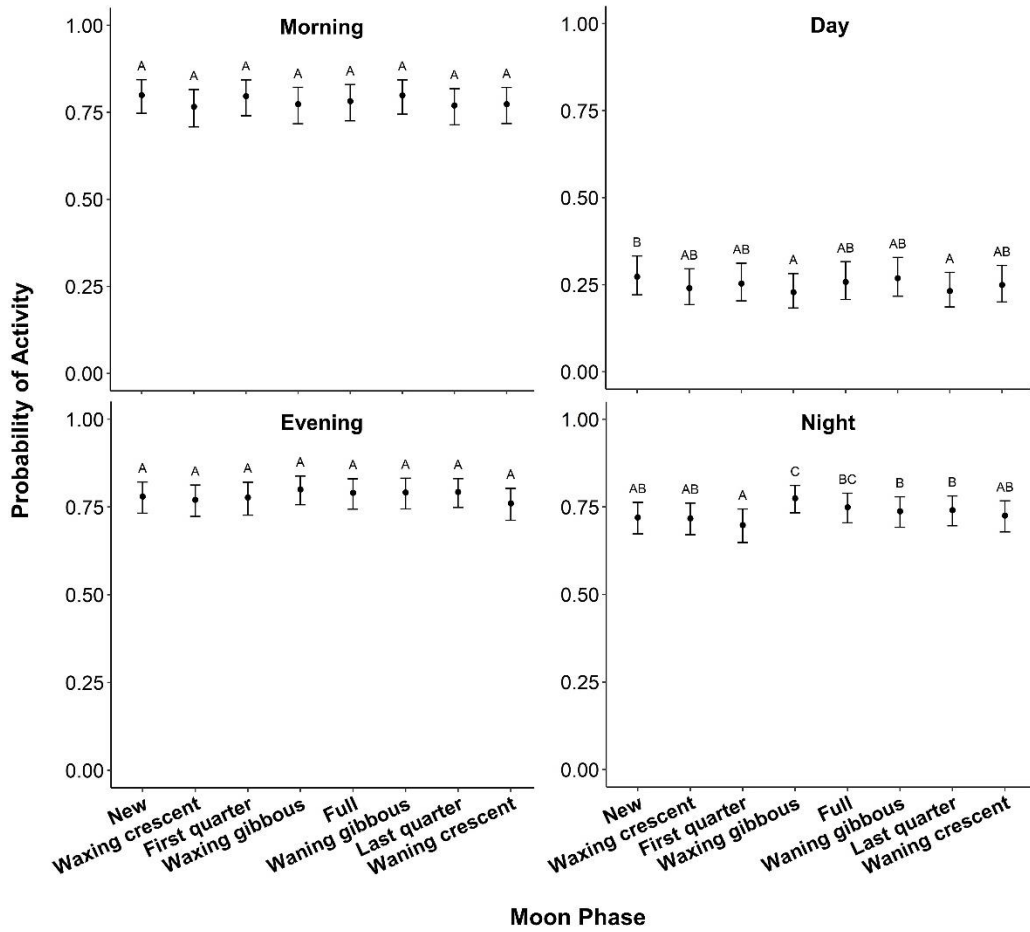
Figure 2.30. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult females during the pre-breeding season (letters indicate statistical significance at α=0.05). Fog was removed from analyses during the evening due to small sample size.
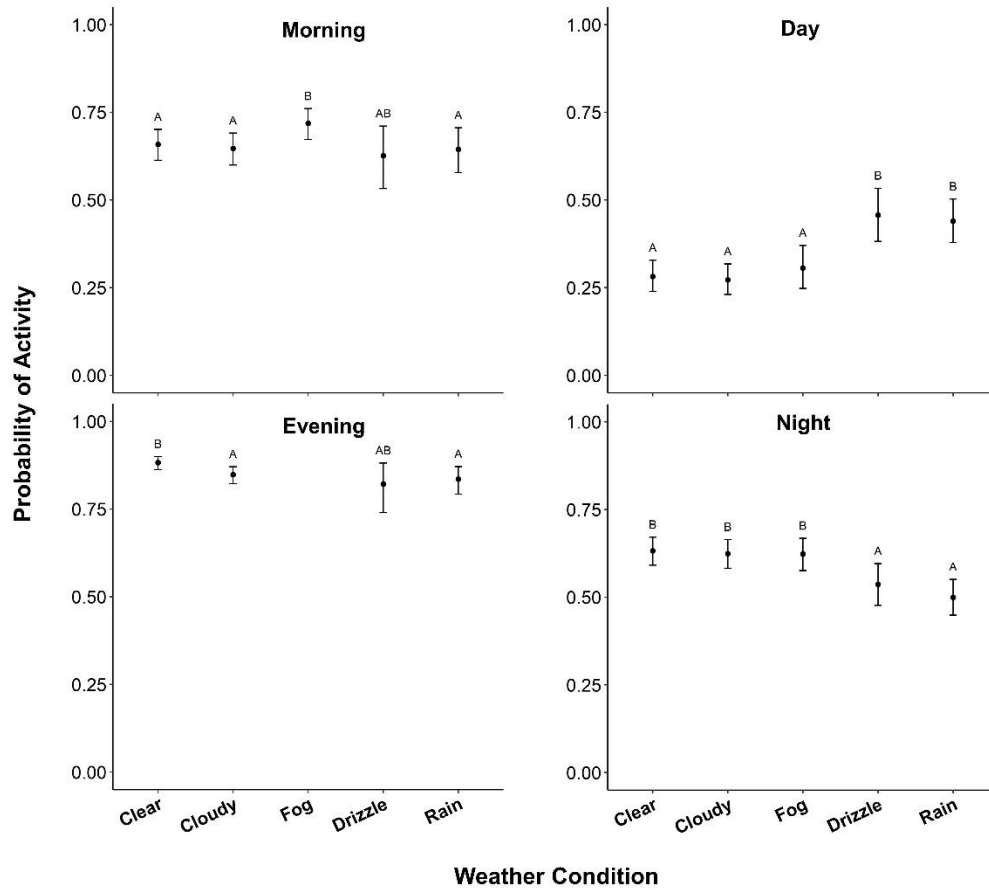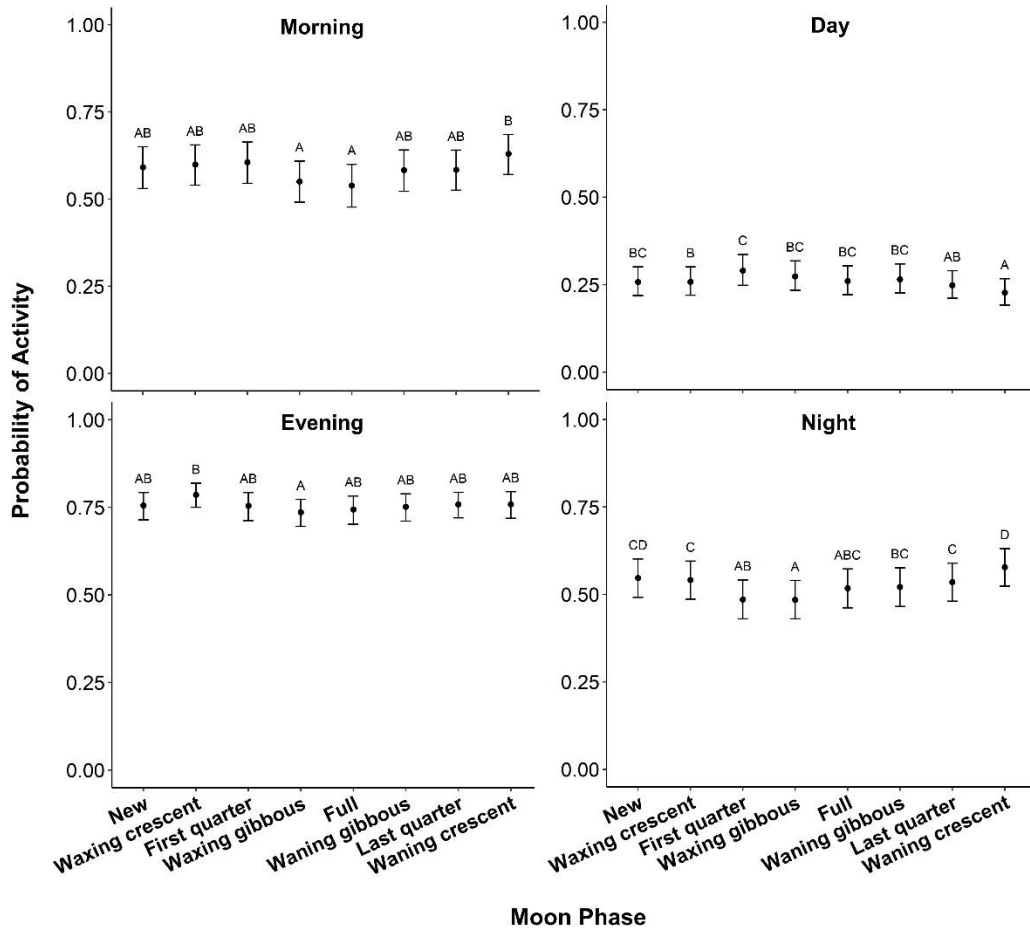
Figure 2.31. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult females during the breeding season (letters indicate statistical significance at α=0.05). Fog was removed from analyses during the evening due to small sample size.

Figure 2.32. Model estimated average probability of activity (95% CL) relative to time of day and weather condition for adult females during the post-breeding season (letters indicate statistical significance at α=0.05).
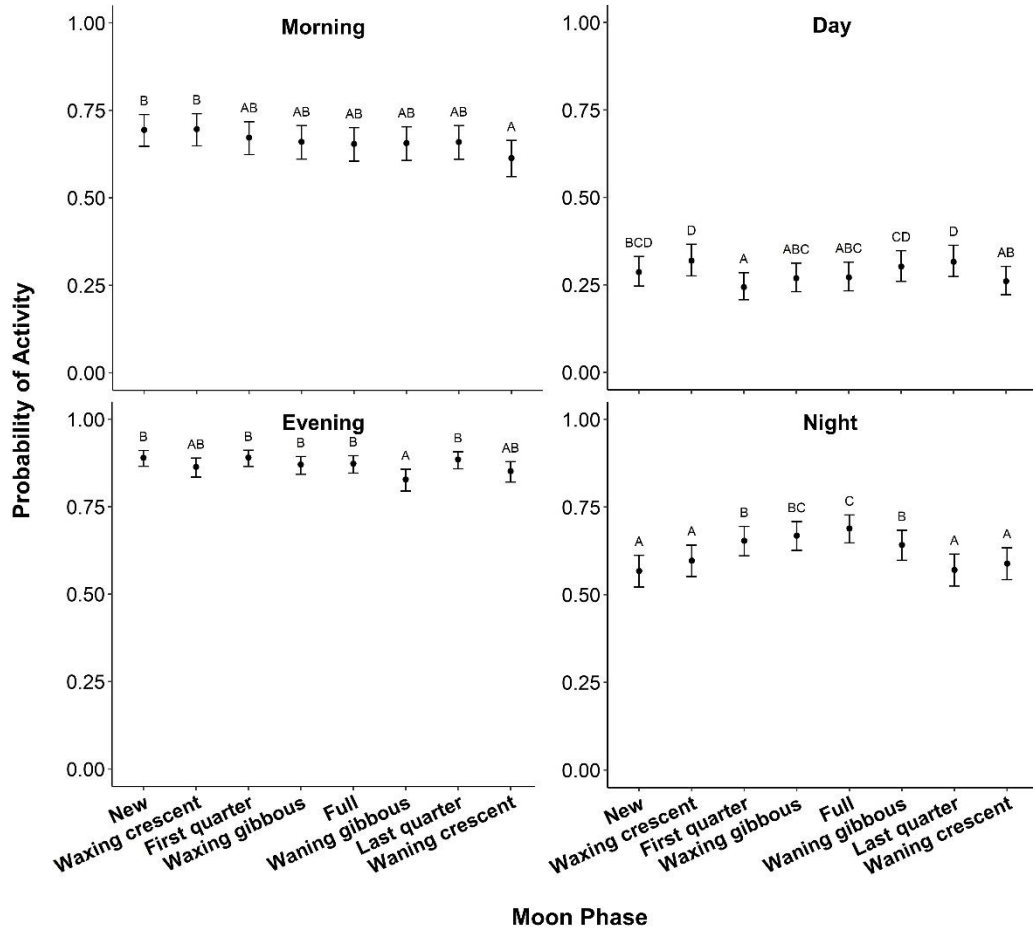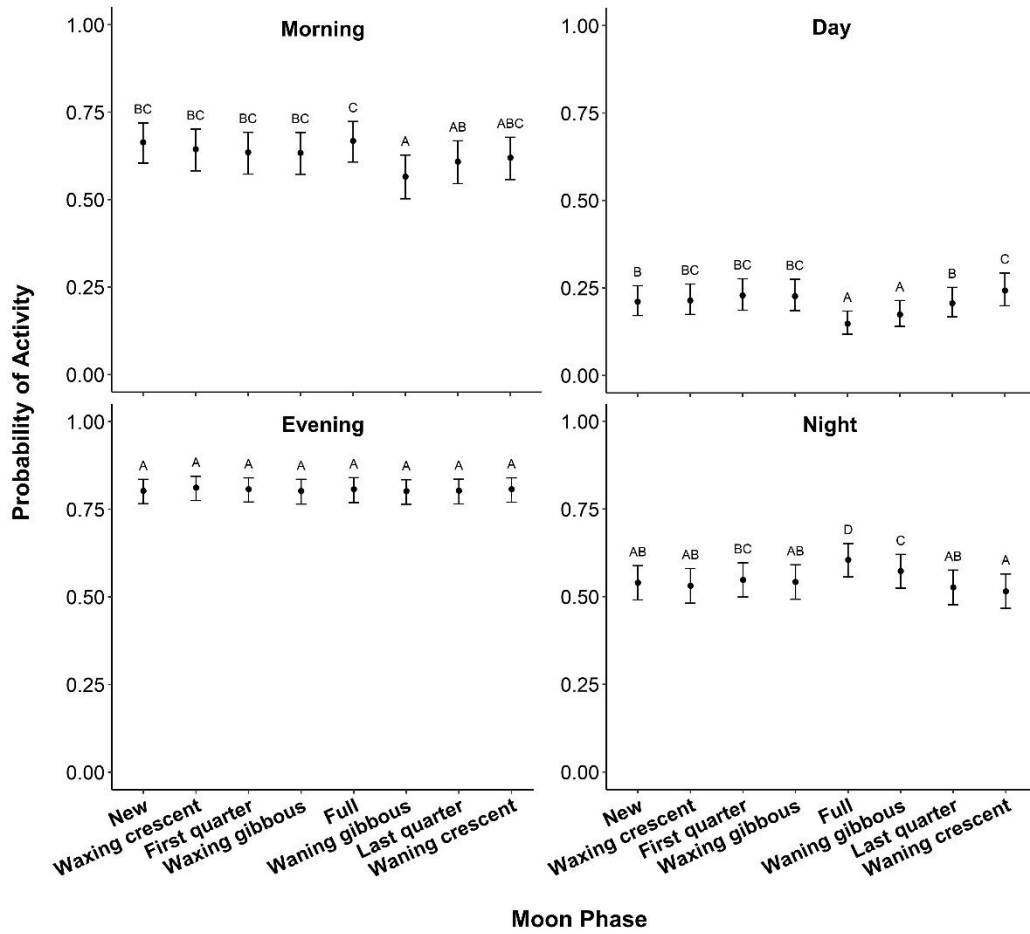
Figure 2.33. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult males during the pre-breeding season (letters indicate statistical significance at α=0.05).

Figure 2.34. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult males during the breeding season (letters indicate statistical significance at α=0.05).

Figure 2.35. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult males during the post-breeding season (letters indicate statistical significance at α=0.05).
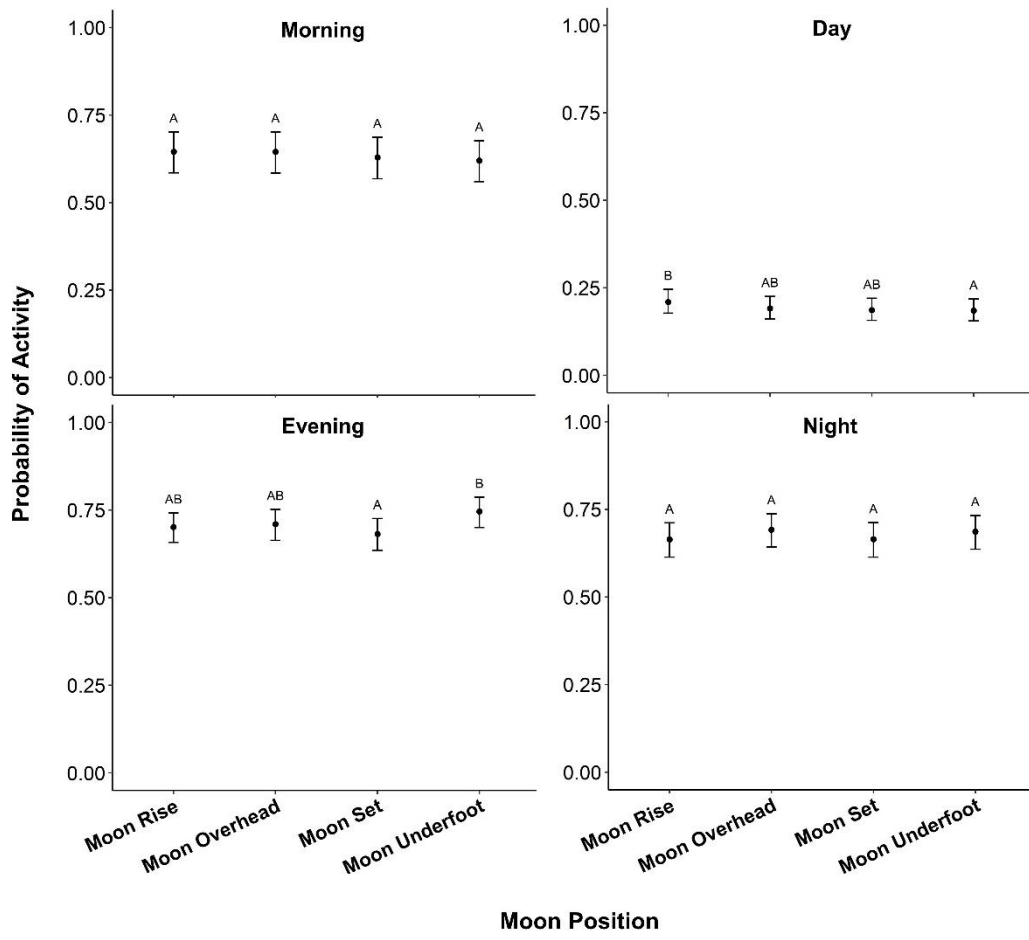
Figure 2.36. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult females during the pre-breeding season (letters indicate statistical significance at α=0.05).
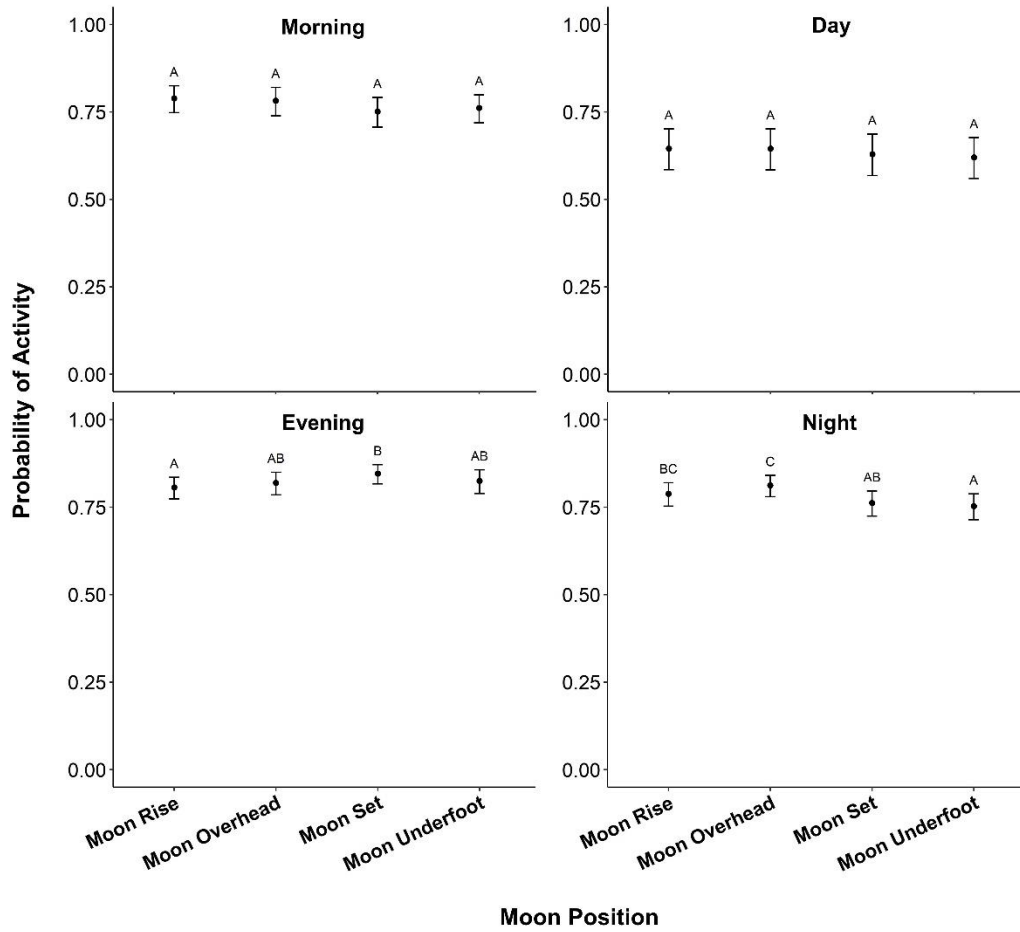
Figure 2.37. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult females during the breeding season (letters indicate statistical significance at α=0.05).

Figure 2.38. Model estimated average probability of activity (95% CL) relative to time of day and moon phase for adult females during the post-breeding season (letters indicate statistical significance at α=0.05).
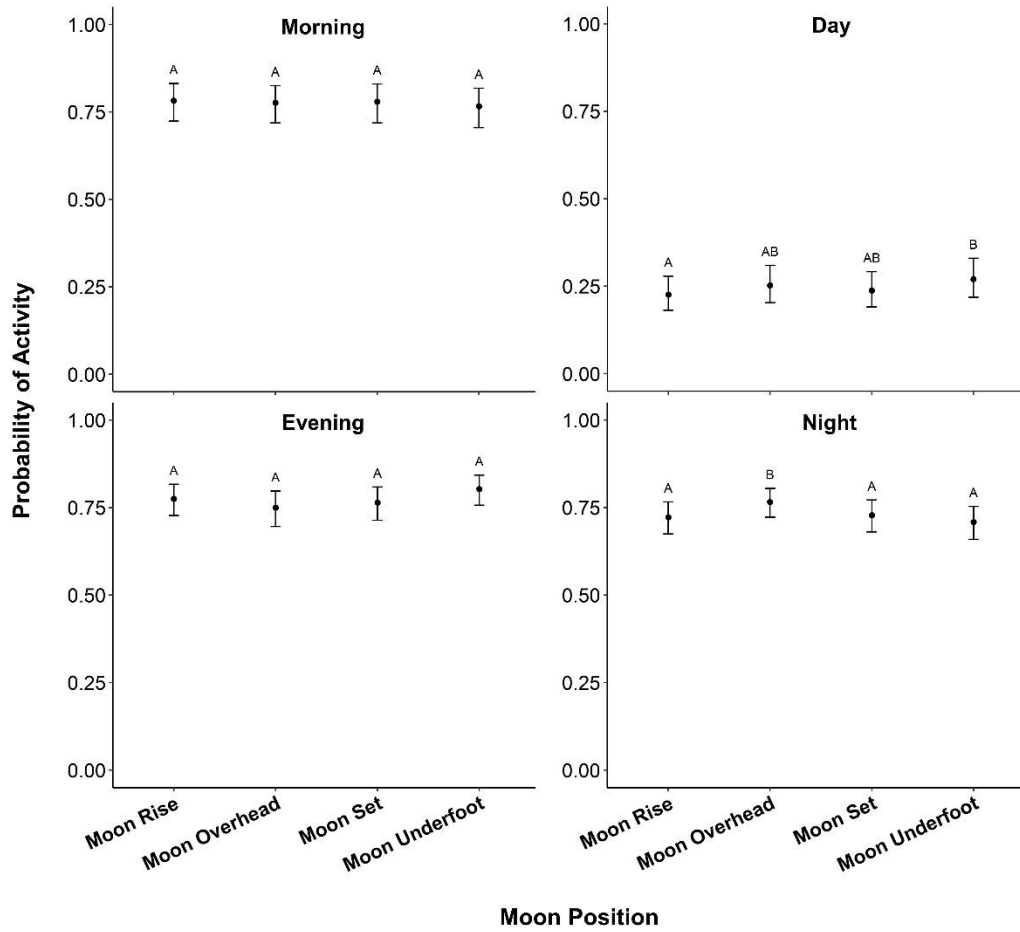
Figure 2.39. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult males during the pre-breeding season (letters indicate statistical significance at α=0.05).

Figure 2.40. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult males during the breeding season (letters indicate statistical significance at α=0.05).
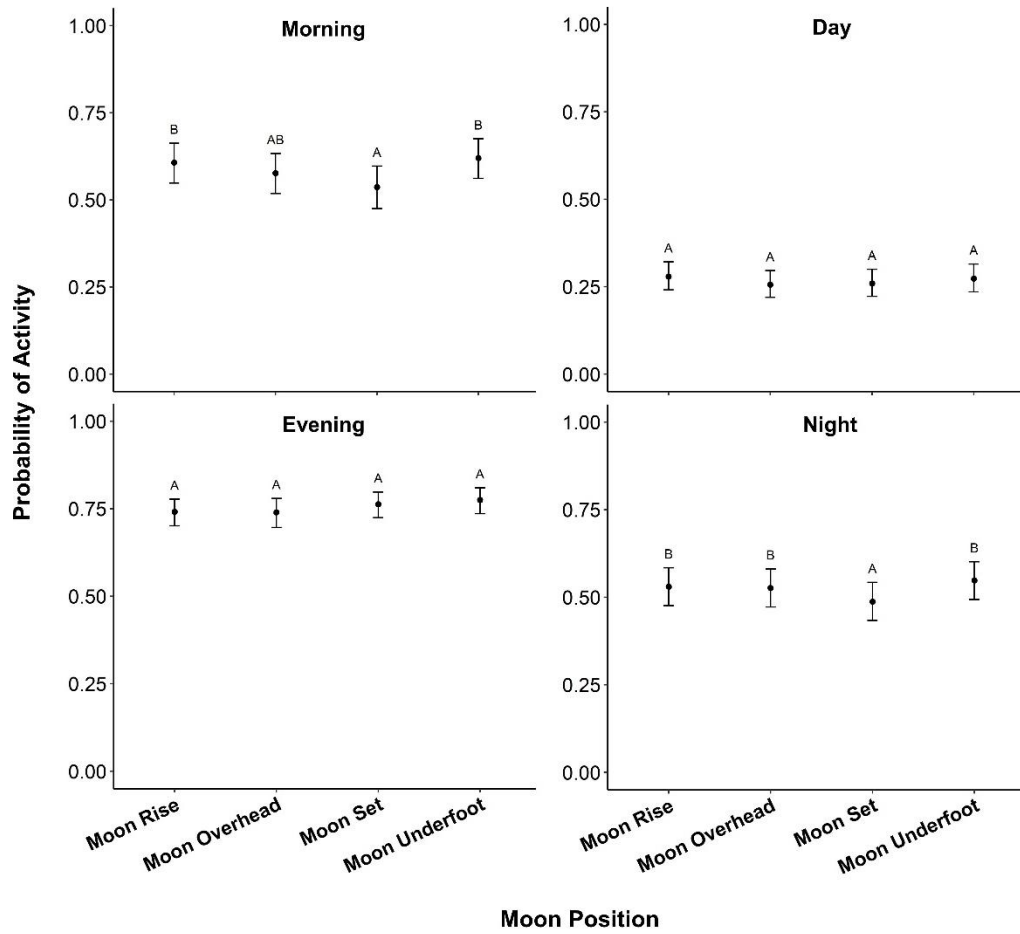
Figure 2.41. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult males during the post-breeding season (letters indicate statistical significance at α=0.05).
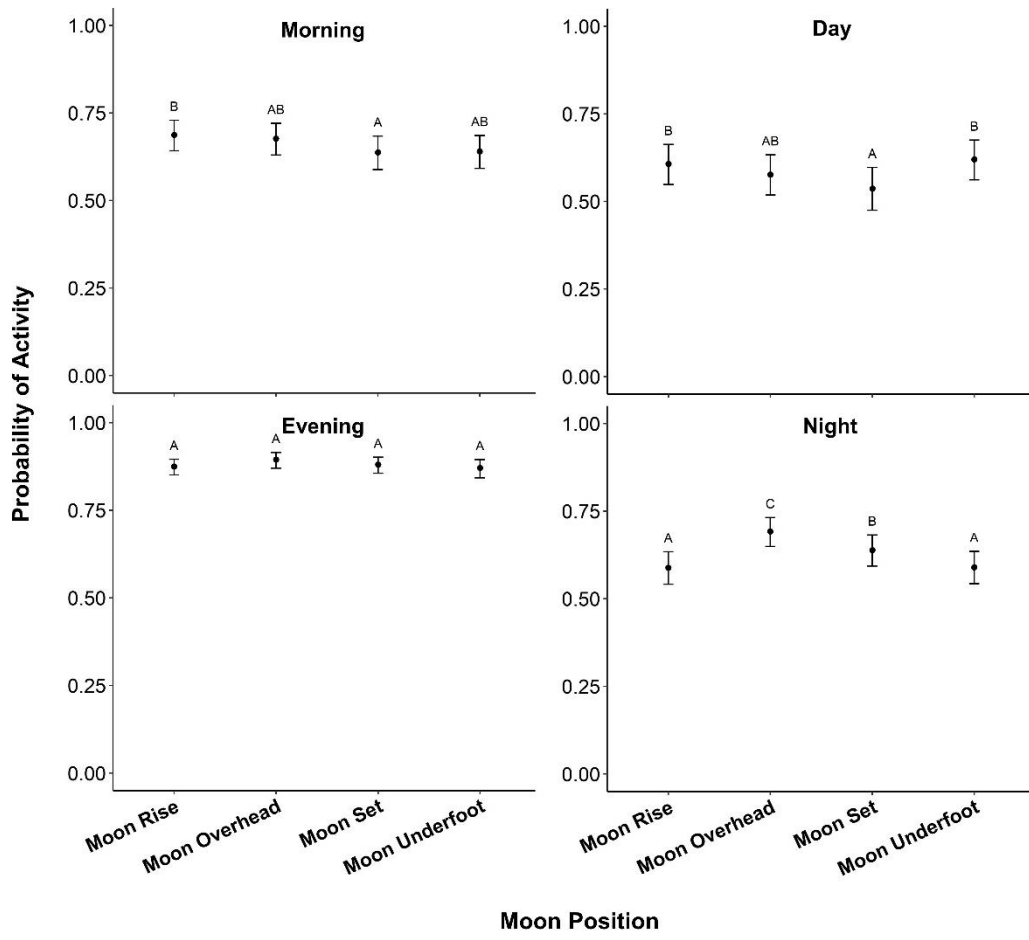
Figure 2.42. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult females during the pre-breeding season (letters indicate statistical significance at α=0.05).

Figure 2.43. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult females during the breeding season (letters indicate statistical significance at α=0.05).
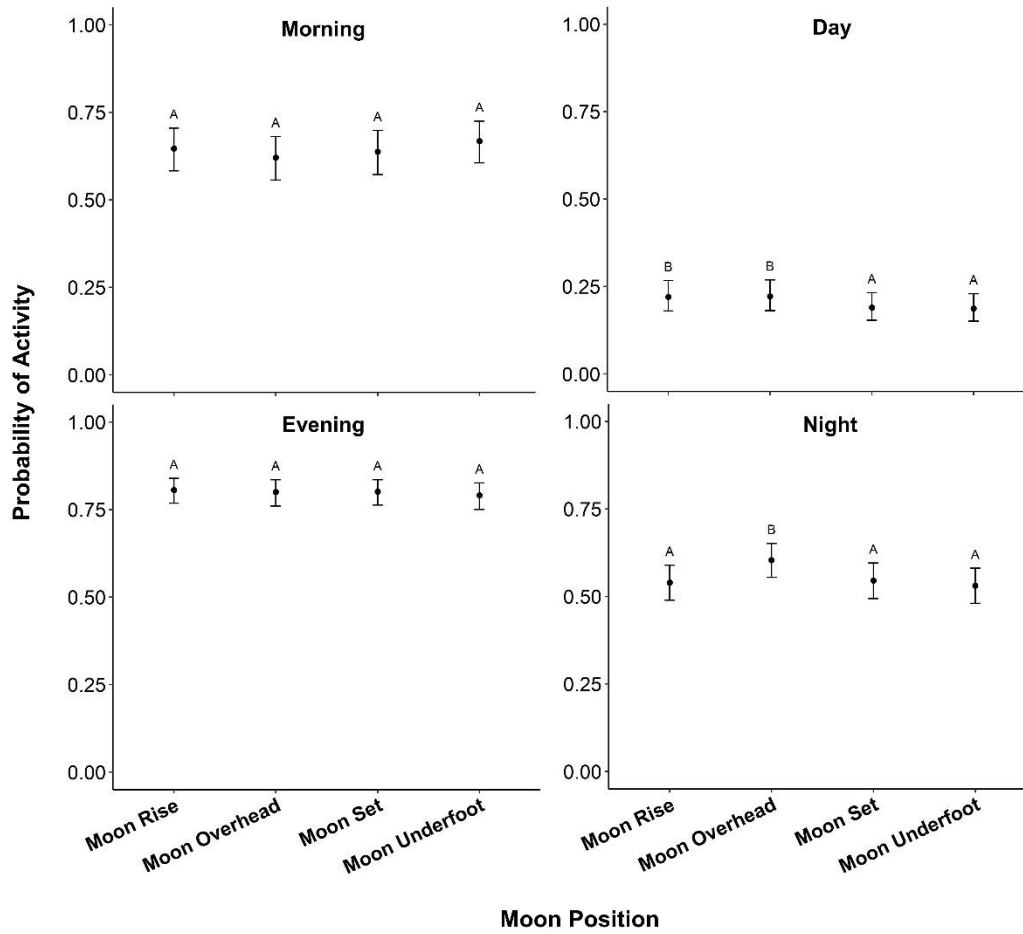
Figure 2.44. Model estimated average probability of activity (95% CL) relative to time of day and moon position for adult females during the post-breeding season (letters indicate statistical significance at α=0.05).