BEHAVIORAL AND SPATIAL ECOLOGY OF WHITE-TAILED DEER IN THE BIG CYPRESS BASIN OF FLORIDA

by

Daniel A. Crawford

(Under the Direction of

Richard B. Chandler and Karl V. Miller)

ABSTRACT

White-tailed deer (*Odocoileus virginianus*) in the Big Cypress Basin of Florida encounter a unique set of abiotic and biotic factors, including seasonal flooding and risk of predation, that affect resource selection and space use. Reported declines in local deer populations in recent years warrants renewed focus on the effects of hydrology and predation on deer populations, particularly in light of increased Florida panther (*Puma concolor coryi*) abundance. To assess the effects of predation risk and seasonal fluctuations in hydrology on the behavioral and spatial ecology of deer, I analyzed camera trap and GPS-telemetry data in the context of the white-tailed deer reproductive cycle and conclude that hydrology and risk of predation by panthers profoundly influence deer behavior and space use as deer attempt to forage optimally under the constraints of predation risk and unpredictable temporal variability in resource availability.

INDEX WORDS: Behavior, Home range, Hydrology, Panther, Predation risk, Resource selection, Sexual segregation, Spatial ecology, White-tailed deer

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by

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DEDICATION

This thesis is dedicated to my wife, Tara, who believed I was capable of seizing my dreams when I did not. I also dedicate this thesis to my mother, Danita, and my father, Alan. Their unwavering support and encouragement have been foundational to my success.

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TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) in southwestern Florida are a valued resource and a primary prey species for the endangered Florida panther (*Puma concolor coryi*) (Maehr et al. 1990). The Big Cypress National Preserve (BCNP) and the Florida Panther National Wildlife Refuge (FPNWR) have witnessed two decades of increasing panther abundance as a result of successful restoration efforts. Simultaneously, efforts to restore hydrological regimes to pre-drainage conditions have resulted in increasing mean water depths since the onset of large-scale drainage operations in 1882 (Loveless 1959a, Booth et al. 2014). Loveless (1959a) suggests that regional drainage efforts facilitated population growth in local white-tailed deer herds by increasing the amount of dry, habitable land. In recent years, hunter harvest data collected by the Florida Fish and Wildlife Conservation Commission (FWC) at hunter check stations on BCNP indicate a significant decrease in deer harvest per hunter effort in portions of the Preserve suggesting populations are in decline in those areas. Similarly, annual aerial surveys conducted by FWC personnel have documented decreases in deer populations. Widespread declines in deer populations would be undesirable for stakeholders, managers, and local predator populations, including the endangered Florida panther. A thorough understanding of the population dynamics and behavioral ecology of white-tailed deer in the Big Cypress Basin (BCB) is needed to develop and execute management strategies aimed at increasing and stabilizing deer populations for sustainable use by humans and local predator populations.

White-tailed deer populations in the BCB are subjected to top-down pressures from a diverse predator community, bottom-up pressures from extreme variability in seasonal and annual resource availability, and anthropogenic forces through human disturbance and harvest. Predators of white-tailed deer in BCB include Florida panthers, Florida black bears (*Ursus americanus floridanus*), bobcats (*Lynx rufus*), American alligators (*Alligator mississippiensis*), as well as novel predators such as coyotes (*Canis latrans*) and the invasive Burmese python (*Python bivittatus*) (Schemnitz 1972; Land 1991; Labisky et al. 1995; Labisky and Boulay 1998; Dorcas et al. 2012). Seasonal hydrology can influence the abundance and distribution of resources, but may also interact with predation by increasing susceptibility to some predators (i.e., American alligators; MacDonald-Beyers and Labisky 2005) and congregating deer near dwindling resources. These factors directly contribute to mortality rates and, potentially, to a declining population trajectory. Indirectly, they influence spatial and temporal resource selection and affect deer populations through reduction of habitat and forage while increasing predation risk. Understanding the effects of predation risk and hydrology on the spatial ecology of deer within the BCB is important given reported declines in deer populations.

Managers rely on the best available science to inform management decisions. Prior investigations that have focused on spatial ecology of deer in southern Florida have relied on the use of aerial very high frequency (VHF) radio-telemetry data generally recorded between 09:00 and 12:00 every 5 days (Schortemeyer et al. 1991, Sargent 1992, Zultowsky 1992, Miller 1993, MacDonald-Beyers and Labisky 2005). The infrequency of data acquisition coupled with the narrow window of flight times lends to bias in habitat selection analyses and may not be representative of how deer utilize resources at the diel or seasonal scale. The recent improvements in reliability, availability, efficiency, and cost-effectiveness of GPS-telemetry allows analysis of fine-scale space use over a broad geographical extent and multiple temporal scales. Furthermore, the increasing prevalence of high-frequency relocation data has driven development of innovative approaches to home range quantification and habitat selection analyses. For example, mechanistic models that predict the utilization distribution as a function of habitat selection have gained traction as researchers question the biological relevance of home ranges estimated by traditional home range methodologies, such as minimum convex polygon (MCP; Kie et al. 2010). The fine-scale, high-resolution data provided by GPS-telemetry also allows for less invasive, more accurate relocation data collection. Coupled with rapidly evolving statistical techniques, such as point process models (e.g., Johnson et al. 2013, Warton and Shepherd 2010) and current Geographical Information System (GIS) technology, these data enable more accurate inferences about animal behavior and space use. This evolving field of spatial ecology allows quantification of the indirect effects that the previously mentioned stressors have on the BCB deer herd, enabling us to inform white-tailed deer management decisions in the context of Florida panthers and interest of public stakeholders.

LITERATURE REVIEW

The home range of an animal has been defined as that area traversed by an individual in its normal activities of food gathering, mating, and caring for young (Burt 1943). When habitat patches are thought of in terms of resource units, it is apparent that resource selection and home range are inherently correlated concepts, and an animal’s home range is a function of its mobility and the spatial resources to which that mobility affords the animal access. White-tailed deer movement and home range size are influenced by various factors including population density, local climate, forage abundance, social behavior, and disturbance (Burt 1943; Sanderson 1966; Sparrowe and Springer 1970; Verme 1973). Home ranges size and composition can be influenced by demographic and seasonal variables. Biological mechanisms often incur different resource demands while variable habitat conditions affect resource availability. For example, female home ranges are most constricted immediately before, and for up to 2 months after, parturition when individuals are selecting fawning sites and subsequently fawn-rearing (Ozoga et al. 1982). Other studies have reported significantly smaller spring and summer male home range sizes attributed to increased forage availability during respective growing seasons of the study sites (Nelson and Mech 1981; Beier and McCullough 1990; Olson 2010). Age also affects space use. Natal dispersal, whereby an individual permanently moves away from its natal range, is unique to immature individuals with yearling males dispersing further and more commonly than yearling females (Downing et al. 1969; Kammermeyer and Marchinton 1976; Long and Diefenbach 2005; McCoy et al. 2005; Long et al. 2008; Nelson and Mech 2008). Understanding space use and resource selection of deer in the context of temporal variability in resource availability is important for making appropriate management decisions.

In southern Florida, the relative importance of resources to white-tailed deer likely varies through time due to seasonal hydrological extremes. Approximately 65% of annual precipitation occurs during summer months typically inundating a majority of the landscape for prolonged periods (Duever 1986). However, drought conditions are not uncommon in winter months resulting in pronounced wet and dry periods that are highly variable in terms of timing, intensity and duration. Despite variable timing, the wet and dry seasons are typically considered from May 1-October 31 and November 1-April 30, respectively. This seasonal hydrology affects many aspects of white-tailed deer ecology in southern Florida, including breeding chronology and space-use. The high annual variation in hydrology can have profound influences on deer demography and habitat selection (Richter and Labisky 1985; Miller 1993; Labisky et al. 1995; Labisky and Boulay 1998; MacDonald-Beyers and Labisky 2005). For example, Sargent (1992) and Miller (1993) found no effect of standing water on deer movement contrary to the conclusions of Flemming et al. (2005) and Loveless (1959a). However, Sargent (1992) and Miller (1993) collected data in years of relatively low precipitation with mean water levels not exceeding 0.3 m. Conversely, MacDonald-Beyers and Labisky (2005) compared years of relatively high and low standing water and documented significant shifts in habitat selection and a 100% increase in mortality rates of radio-collared deer in 1994-1995, a year of record high water (mean water level = 0.73 m). Specifically, they observed strong selection for hardwood hammock “islands”, which remained relatively dry. Use of GPS-telemetry and evolving analytical techniques present opportunities to gather and analyze fine-scale spatiotemporal data necessary to evaluate habitat-specific effects of seasonal flooding on selection and home range size of deer.

While seasonal inundation may affect space use at a broad temporal scale, risk of predation must be continuously assessed by prey species as they make behavioral decisions about when and where to forage in the context of spatiotemporal variability in risk. Predators directly affect prey populations by removing individuals from the population and indirectly by inducing morphological, physiological, and behavioral shifts in response to the risk of predation (McCollum and Leimberger 1997; Brown 1999; Clinchy et al. 2013). Prey behaviorally mitigate risk by changing rates of vigilance, patterns of activity, or space use. While mortality of white-tailed deer attributed to direct predation has been well documented in the south Florida system

(Beier and McCullough 1990; Land 1991; Miller 1993; Labisky and Boulay 1998; Beier et al. 2003), these studies occurred prior to or shortly after the genetic restoration of the endangered Florida panther (*Puma concolor coryi*). In 1995, 8 wild-caught female puma from Texas were released in southern Florida for genetic introgression purposes. Since that time, the panther population has increased 600%, from 20-30 individuals to a minimum of 130 adults. How the increase in panther abundance affects deer in terms of both direct and indirect effects is unknown. Furthermore, evidence suggests the indirect effects of a predator may be predicted by the hunting mode of the predator (Lingle 2001; Lingle and Wilson 2001; Stankowich and Coss 2007). Sit and pursue and ambush predators such as panthers may have greater non-consumptive effects on their prey than wide-ranging cursorial predators because informative habitat cues (e.g., edge) can be associated with risk (Schmitz 2008). To date, no studies have addressed the indirect effects of predation on deer in the Florida panther range, particularly as related to habitat selection. The coupled effects of hydrology and increased predation risk may drive habitat selection and avoidance patterns of white-tailed deer in southern Florida.

Predation risk has also been hypothesized as a driver of sex-specific habitat selection in polygynous ungulates as the sexes experience differing energetic demands in the context of reproductive processes (Main et al. 1996). For male deer, reproductive opportunity is positively correlated with body mass, and the breeding season represents the most reproductively important time period. While nutritional status of females is positively correlated with fecundity (Verme 1969), nutritional state does not affect female breeding opportunity. However, females are most energetically burdened during the fawn-rearing season when lactation incurs nutritional costs (Oftedal 1985). Additionally, females must make behavioral decisions under the risk of predation such that they adequately meet energetic intake requirements while minimizing exposure to risk, especially when offspring are most vulnerable to predation. The reproductive-strategy hypothesis, also referred to as the predation risk hypothesis by Ruckstuhl and Neuhaus (2000), links sex-specific variability in energetic demand across biological seasons with behavioral decision-making under the risk of predation. Thus, under the reproductive strategy hypothesis, the sexes are predicted to exhibit the greatest segregation during the fawn-rearing season. Females are predicted to select the safest habitat that provides sufficient resources during fawn-rearing, and are expected to exhibit greater site fidelity to smaller areas as a function of predictable resource availability (Main et al. 1996). While numerous hypotheses attempt to explain the causal mechanism of sexual segregation, non-mutually exclusive hypotheses and a lack of overwhelming support for a single hypothesis suggest that segregation between the sexes is likely context-specific with respect to a species' life history, predator-community, and site-specific environmental factors (Main et al. 1996; Barboza and Bowyer 2000; Ruckstuhl and Neuhaus 2000; Main 2008). Evaluating space use of deer in the BCB affords opportunity to uniquely test the reproductive-strategy hypothesis in the context of seasonal hydrology and spatiotemporal variation in risk of predation.

The deer population of southern Florida has been the focus of numerous research projects, however shifts in the hydrological regime, restoration of local predator populations, and increasing populations of novel predators such as coyotes and pythons have potentially altered population dynamics of local herds. Urgency to understand these factors is increasing with reported decreases in some deer populations across the region. Growing panther populations further intensify this urgency as state and federal agencies aim to maintain local white-tailed deer populations.. My research is intended to inform agency management plans in an effort to ensure the availability of white-tailed deer populations as a resource for both humans and the endangered Florida panther.

STUDY SITE

The Big Cypress Basin (BCB) of southwestern Florida is characterized by a seasonal tropical climate with hot summers accounting for more than 60% of annual rainfall and relatively dry, mild winters creating distinct wet and dry seasons (Hela 1952; Harlow 1959; Loveless 1959b; Duever 1986). Temperatures range from 14-28°C with an annual mean temperature of 23°C (Duever 1986). Regional topography has minimal relief with slight ridges delineating relatively flat basins interspersed with depressions that retain standing water throughout the dry season (Loveless 1959b, Duever 1986). A 9 cm/km slope to the southwest induces a southwestern sheet flow of water across the landscape. Low relief along with warm season precipitation characteristic of the regional climate contribute to seasonal inundation of much of the landscape with mean water depths ranging from 0.3-0.73m (Duever 1986).

Five vegetation communities dominate the BCB including pine forests, hammock forests, cypress forests, prairies, and marshes (McPherson 1974). Pine forests are dominated by slash pine (*Pinus elliottii*) with an understory of cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), and evergreen shrubs. Grasses are the dominant ground cover in these pine forests. Hammock forests are found on areas of higher elevation and are composed of hardwoods, palms, ferns, and shrubs (McPherson 1974). Cypress communities are found at lower elevations and vary in composition from open stands of cypress (*Taxodium distichm*) varying in size with minimal herbaceous growth interspersed to mixed swamps with dense tangles of trees, vines, shrubs, and epiphytes and are indicative of drainage areas (Harlow 1959;

Harlow and Hooper 1971; Duever 1986). Both types of prairie, wet and dry, are dominated by grasses with few trees, however, wet prairies are a mixture of prairie and marsh communities. Lastly, marshes are characterized by emergent wetland vegetation such as sawgrass (*Cladium mariscus*) and rushes (*Juncus* spp.) with alligator flag (*Thalia geniculata*) dominating deeper depressions. Typical water depths in marshes are several inches deeper than surrounding wet prairies and swamps (McPherson 1974).

OBJECTIVES

Using infrared-triggered camera trap data and GPS-telemetry relocation data, I investigated the behavioral and spatial ecology of white-tailed deer in the Big Cypress Basin of Florida to achieve these objectives:

1) Determine the sex-specific behavioral effects of predation risk on activity patterns of white-tailed deer.
2) Characterize sex-specific space-use and resource selection of white-tailed deer populations.
3) Evaluate the influence of predation risk and hydrology on resource selection and home range size of white-tailed deer.

THESIS FORMAT

This thesis is presented in manuscript format. Chapter 1 presents the introduction and literature review pertinent to topics discussed in this thesis. Chapter 2 presents data and analyses demonstrating sex-specific, seasonally variable behavioral responses of white-tailed deer to risk of predation via two analyses of camera trap data: (1) results from detection rate analysis indicate avoidance of activity in areas and during times characterized by high risk of predation, and (2) temporal overlap in activity patterns of deer and panthers is greatest during periods of respective reproductive importance to the deer sexes. Chapter 3 describes seasonal space-use of white-tailed deer in the context of home range size and spatial resource selection, and addresses the effects of hydrology and risk of predation on deer spatial ecology. Chapter 4 provides general conclusions, management implications, and prospective topics for future research.

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CHAPTER 2

SEX-SPECIFIC BEHAVIORAL RESPONSES OF WHITE-TAILED DEER TO THE RISK OF PREDATION BY FLORIDA PANTHERS [1]

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[1] Crawford, D. A., M. J. Cherry, B. D. Kelly, E. P. Garrison, D. A. Shindle, L. M. Conner, R. B. Chandler, and K. V. Miller. To be submitted to *Behavioral Ecology*

ABSTRACT

The effects of predators on prey populations can be categorized as direct, consumptive effects or indirect, non-consumptive effects (NCEs). Consumptive effects are the result of lethal encounters whereby predators remove individuals from the population. Alternatively, NCEs are physiological and behavioral responses of prey to the risk of predation, such as shifts in spatiotemporal movement patterns. To assess the non-consumptive effects of a mammalian ambush predator on its primary prey, we examined the activity patterns of sympatric white-tailed deer (*Odocoileus virginianus*) and Florida panthers (*Puma concolor coryi*) by comparing diel detection rates of both species at 180 motion-triggered camera traps positioned on (*n* = 120) and off (*n* = 60) of off-road vehicle (ORV) trails from February-October 2015. Unlike most regions of their range where white-tailed deer are nocturnal or crepuscular, we found that 79% of deer detections occurred between sunrise and sunset compared to 28% for panthers. This temporal shift in activity patterns appears to be a response to the activity of panthers, which were detected most often (72% of detections) at night. Our data indicate that peak deer activity in south Florida occurs during daylight in a hot, tropical climate where thermoregulatory costs associated with diurnal activity should be relatively high. Furthermore, our results suggest that deer perceive ORV trails as high-risk areas and reserve activity on trails for relatively low- risk diurnal hours. We provide evidence supporting the hypothesis that fear of predation by panthers influences when and where white-tailed deer choose to be active as they attempt to forage optimally in the context of spatially and temporally variable risk of predation.

INTRODUCTION

Predators impact prey populations directly through mortality or indirectly through non-consumptive predation risk effects. Morphologically, predators may induce phenotypic shifts in prey. Physiological responses of prey to risk of predation also affect prey demography as elevated risk of predation can suppress reproductive rates and decrease survival by indirectly altering metabolic processes (Clinchy et al. 2004; Sheriff et al. 2009; Travers et al. 2010; Zanette et al. 2011). Furthermore, prey populations may experience residual physiological effects in the absence of predators as a result of maternal programming (Sheriff et al. 2010; Storm and Lima 2010). In addition to affecting morphology and physiological processes, predators also influence prey behavior as individuals attempt to optimize foraging such that energetic intake is maximized and risk is minimized. Brown et al. (1999) reviewed behavioral effects of predation risk such as shifts in space use, temporal activity patterns, and rates of vigilance, and suggested that such effects pervade behaviorally responsive predator-prey systems. To fully understand the interactions between predators and their prey, it is important to consider the cumulative impacts of both consumptive and non-consumptive interactions.

Animals must balance energy and activity budgets (Lima 1998), particularly when energetically profitable forage patches also impose the greatest risk of predation (Werner and Anholt 1993). In these situations, animals must decide when, where, how, and how long to forage based on their assessment of the risk of predation (Lima and Dill 1990). Brown et al. (1999) describe the “ecology of fear” as a framework for understanding the trade-offs faced by prey populations. By expanding optimal foraging theory to include predation risk, they propose a classification scheme that delineates N-driven (mortality driven) from µ-driven (behaviorally driven) predator-prey systems (Lima and Dill 1990). Laundré et al. (2001) expanded on this concept and described the “landscape of fear” as spatiotemporal variability of predation risk that structures communities across landscapes where variation in predation risk can be conceptualized as contours superimposed over the landscape. Quantification of trade-offs posed by predation risk, or “mapping the landscape of fear”, has relied heavily on comparison of vigilance rates and giving-up densities (GUDs) in the context of categorical habitat patches or features (Brown 1988; Altendorf et al. 2001; Hernandez et al. 2005; Rieucau et al. 2009; Cherry et al. 2015). However, these methodologies require artificial food resources and may not effectively delineate predation risk effects from behavioral effects induced by social phenomena such as dominance hierarchies (e.g., Lashley et al. 2014), particularly in sexually dimorphic ungulates.

Sex-specific anti-predator behaviors in sexually dimorphic ungulates have remained a point of interest in attempting to understand sexual habitat segregation. Factors believed to influence sexual segregation include morphological variation (Barboza and Bowyer 2000), reproductive strategy/predation risk (Bleich et al. 1997), and social factors (Pérez-Barbería et al. 2005), however the evidence is equivocal and no single hypothesis has garnered overwhelming support. Regardless of the driving force behind sexual segregation, the behaviors of males and females of polygynous ungulates differ substantially (Bowyer 2004). For males, body size is positively correlated with breeding success (Townsend and Bailey 1981; DeYoung et al. 2006). For females, nutritional status is positively correlated with maternal investment in offspring (Therrien et al. 2008). However, predation risk also must be considered to understand ungulate fitness because both sexes must attempt to optimize energetic intake under risk of predation according to their respective reproductive physiologies and energetic demands (Mech and Peterson 2010). Therefore, risk of predation may result in sex-specific behavioral decisions that differentially impact the relative fitness of males and females. Further, relative paternal and maternal investment in offspring should contribute to sexual divergence in behavioral decision-making because females bear sole responsibility for rearing offspring.

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are a model species for behavioral investigations of sexually segregated polygynous ungulates. The species' expansive range and high abundance have afforded investigators the opportunity to study anti-predator behaviors in the context of region-specific factors such as climate, habitat, and predator community. From the boreal forests of Canada populated by wolves (*Canis lupus*) to the tropical rainforests of South America inhabited by puma (*Puma concolor*) and jaguar (*Panthera onca*), a robust literature describes anti-predator responses including grouping behavior, flight distance, alarm signaling, vigilance, giving-up densities, and shifts in space use (Hirth and McCullough 1977; Messier and Barrette 1985; LaGory 1987; Lingle 2001; Rieucau et al. 2009). However, little is known about how deer behaviorally negotiate variability of predation risk across the landscape at both diel and seasonal time scales. Understanding spatiotemporal behavioral responses to predation risk is further complicated by predator-specific traits that affect the magnitude of response in prey. For example, ambush predators are predicted to induce risk effects of greater magnitude than active, cursorial predators due to the association of the predator with habitat cues (Preisser et al. 2007; Middleton et al. 2013).

The restoration of the endangered Florida panther (*P. c. coryi*; hereafter panther), an efficient ambush predator of adult deer, in southwestern Florida provides an opportunity to investigate behavioral responses of deer to predation risk that varies in space and time. Since 1995, the panther population increased 14% annually from an estimated 20-25 to a minimum of 130 by 2015 (Johnson et al. 2010; Florida Fish and Wildlife Conservation Commission 2015).

The recovery of large carnivores has been shown to induce shifts in ungulate behavior (Berger et al. 2001; Laundré et al. 2001; Creel et al. 2005; Kauffman et al. 2007). Middleton et al. (2013) documented relatively weak risk effects of wolves on elk (*Cervus elaphus canadensis*) in the Greater Yellowstone Ecosystem following restoration of the cursorial predator. However, no attention has been given to risk effects associated with the restoration of an ambush predator. Furthermore, few studies have employed the use of remote-sensing cameras distributed at high densities and broad distribution to concurrently monitor predator and prey.

We examined the effects of spatial and temporal variation in panther predation risk on activity patterns of male and female deer. We tested the hypothesis that predation risk would induce sex-specific differences in spatiotemporal activity patterns in the context of variation in predation risk as determined by spatial ('risky places hypothesis') and temporal ('risky times hypothesis') variation in panther activity. High-risk scenarios were characterized by relatively high panther activity. We hypothesized that temporal variation in predation risk would interact with biological season such that deer activity would be greater at high risk times during biological seasons of reproductive importance. Similarly, we hypothesized that spatial variation in predation risk would interact with biological season such that deer activity would be greater in high risk places during biological seasons of reproductive importance. Specifically, we predicted that males would be more active than females in high risk scenarios across all biological seasons and be more risk prone during the breeding season when searching for receptive females. Furthermore, because male reproductive success is positively correlated with body mass (Townsend and Bailey 1981), we predicted that they would make riskier decisions than females immediately before the breeding season to enhance body mass. We predicted females would increase activity in high risk scenarios during the fawn-rearing season when individuals are investing in the energetically demanding process of lactation (Oftedal 1985).

METHODS

Study area

The Big Cypress Basin (BCB) of southwestern Florida is characterized by a seasonal tropical climate with hot summers accounting for more than 60% of annual rainfall and relatively dry, mild winters creating distinct wet and dry seasons (Hela 1952; Harlow 1959; Loveless 1959; Duever 1986). Temperatures ranged from 14-28°C with an annual mean temperature of 23°C (Duever 1986). Minimal relief characterized regional topography with slight ridges delineating relatively flat basins interspersed with depressions that retain standing water throughout the dry season (Loveless 1959b; Duever 1986). A 9 cm/km slope to the southwest induced a southwestern sheet flow of water across the landscape. Low relief along with warm season precipitation characteristic of the regional climate contributed to seasonal inundation of much of the landscape with mean water depths ranging from 0.3-0.73 m (Duever 1986).

Five vegetation communities dominated the BCB including pine flatwoods, hardwood hammocks, cypress swamps, prairies, and marshes (McPherson 1974). Pine flatwoods forests are dominated by slash pine (*Pinus elliottii*) with an understory of cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), and hardwood shrubs. Ground cover in pine flatwoods consisted primarily of grasses. Hammock forests existed on areas of higher elevation and consisted of hardwoods, palms, ferns, and shrubs (McPherson 1974). Cypress communities existed at lower elevations and varied in composition from open stands of cypress (*Taxodium distichm*) varying in size with minimal herbaceous growth interspersed to mixed swamps with dense tangles of trees, vines, shrubs, and epiphytes and are indicative of drainage areas (Harlow 1959; Harlow and Hooper 1971; Duever 1986). Both types of prairie, wet and dry, consisted of grasses with few trees, however, wet prairies included a mixture of prairie and marsh communities. Lastly, emergent wetland vegetation such as sawgrass (*Cladium mariscus*) and rushes (*Juncus* spp.) dominated marshes with alligator flag (*Thalia geniculata*) dominating deeper depressions. Typical water depths in marshes exceeded that of surrounding wet prairies and cypress communities by several centimeters (McPherson 1974).

The study occurred on the adjacent Florida Panther National Wildlife Refuge (FPNWR) and the Bear Island (BI) and Northeast Addition Lands (AL) units of Big Cypress National Preserve (BCNP) (Fig. 2.1). The areas of FPNWR, BI, and AL encompassed approximately 100 km^2, 190 km^2, and 271 km^2, respectively. Public accessibility differed among sites. Bear Island contained a network of off-road vehicle (ORV) trails for public use by permit, and licensed hunting was permitted. Similarly, AL allowed public recreational access, but prohibited ORV access and limited issuance of hunting permits. The FPNWR prohibited public access, although it contained an extensive network of ORV trails to facilitate management activities. All sites contained ORV trail networks, however the intensity of vehicular traffic on and maintenance of trails was variable. For example, regulation restricted vehicular access in AL to authorized administrative personnel who utilized the trail network infrequently for maintenance and wildfire containment purposes.

Study species

White-tailed deer undergo seasonal physiological and behavioral changes associated with the reproductive cycle. Because deer activity is closely linked to reproductive stage, we organized our study in the context of biological seasons of deer in the BCB (Richter and Labisky

1985). Camera trap data indicated a broad window of fawning across most of February and March (Engebretsen, KN, *unpublished data*), thus we designated these months as the fawning season. This timescale was chosen to appropriately characterize behaviors leading up to fawning, such as fawning site selection, while including the time period over which the majority of fawns were born. Because most fawns on our study site were born by the end of March and nearly all bucks had initiated antler growth by this point, we designated April-June 2015 as the fawn-rearing and antler growth season (hereafter rearing). Rearing is an energetically expensive time for reproductive females as fawns grow and lactation peaks (Moen 1978; Pekins et al. 1998). Similarly, males invest in antler development and body growth during this period because antler size and body mass are positively correlated with dominance and reproductive opportunity (Clutton-Brock 1982; DeYoung et al. 2006). We designated July as the pre-rut when males exhibit hyperphagy, increased activity, and increased antler sparring in preparation for conspecific competition. Given the relatively broad fawning window, some breeding occurred through August and September, however peak breeding, or rut, behavior occurred in mid- to late August. This is a stressful time for males as they forage minimally and maximize mate searching behaviors. Following the rut, males enter a recuperation phase known as the post-rut, and bred females are in the earliest stages of gestation during this time.

Camera trap array

We deployed 180 remote-sensing infrared-triggered cameras (HCO Outdoor Products, Norcross, GA, USA) without bait or any attractant across the study area in three grids of 60 cameras (Fig. 2.1). We placed camera grids within a 29 km^2 rectangular region separated by $\geq$ 13 km. We placed 40 cameras in each grid on ORV trails and the remaining 20 approximately 250 m from the trail. We determined on-trail camera trap (henceforth, trap) locations by overlaying aerial photography with 700 m^2 grid cells using ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, CA, USA) and placing traps near the center of cells to maintain an approximate distance of 700 m between on-trail traps. We positioned on-trail traps on the closest suitable tree and oriented each perpendicular to the trail. To maximize probability of detection of animals at off-trail traps, we deployed traps on the most well defined wildlife trail or habitat edge within 50 m of the selected point. We positioned cameras approximately 0.30 m above ground, oriented either north or south, and adjusted height according to surface water levels to avoid inundation. We visited traps at approximately 30 day intervals for data retrieval and camera maintenance, and vegetation was cleared as needed to minimize false-triggering of cameras.

Data Preparation and Analysis

To maximize independence of detections, we sorted records chronologically by camera, and omitted records with the same sex, age, and species class as the previous record from analysis if the time from the previous record was < 6 min. We determined this threshold by filtering the data at 1 minute intervals and plotting the mean difference in time between images (Figure 2.2). The resulting curve indicated a rapid decease in rate of change in the mean interval when images separated by 5 min or less were omitted. This procedure improved independence of detections by removing sequential images of lingering individuals. We then classified detections based on biological seasons and characterized each as either diurnal (between sunrise and sunset) or nocturnal (between sunset and sunrise). Package maptools (Bivand and Lewin-Koh 2015) in Program R (R Core Team 2014) was used to determine daily sunrise and sunset times associated with the coordinates of the centroid of our study area.

We evaluated the effects of panther predation risk on deer activity patterns using the camera trap data. We estimated predation risk by modeling panther activity patterns to predict when and where a deer is likely to encounter a panther. We analyzed count data of bucks, does, and panthers at each camera using Poisson generalized linear mixed models (GLMM) with a log link. The response variable (y_{ijk}) was the number of detections at each camera ($i = 1, \ldots, 180$), during each time period ($j = 1, 2$; for diurnal and nocturnal) and biological season ($k = 1, \ldots, 5$; for fawning, rearing, pre-rut, rut, and post-rut). Explanatory variables included trail (i.e. on- and off-trail), time, and biological season. We fit GLMMs for each sex of deer and a single model for both sexes of panther. We constructed 4 candidate models representative of specific hypotheses, and we used AIC for model selection. Candidate models included various combinations of the main effects of trail, time, and biological season as well as 2-way interactions of each. We hypothesized that time and biological season would interact such that deer detection rates would be greater at high risk times during biological seasons of reproductive importance. Similarly, we hypothesized that trail and season would interact such that deer detection rates would be greater in high risk places during biological seasons of reproductive importance. The number of camera hours varied among scenarios due to variable season and day length (e.g., nocturnal on-trail during the fawning season) and among cameras due to camera failure, which we accounted for by using log(camera hours) as an offset in the GLMMs. As a result, the estimates can be interpreted as the number of detection per hour. We modeled variation among cameras using camera-specific random effects. Due to difficulty of deriving asymptotic standard errors from linear models including random effects, we calculated 95% confidence intervals (CI) for detection rates via parametric bootstrapping, and deemed detection rates of bucks, does, and panthers significantly different when CIs for differences in means did not include zero. We conducted detection rate analyses in program R using package lme4 (Bates et al. 2015).

To test for differences in activity overlap of deer with panthers, we calculated the coefficient of overlap in activity patterns of male and female deer with panthers using non-parametric kernel density estimation of detection times (Ridout and Linkie 2009). We employed nonparametric bootstrapping to calculate confidence intervals for estimates of activity overlap. We estimated sex-specific deer-panther activity overlap for every combination of trail (i.e. on, off) and biological season (i.e. fawning, rearing, pre-rut, rut, and post-rut). We identified significant differences in activity overlap using CIs in the same manner as described for detection rates. We conducted activity pattern overlap analyses in program R using package overlap (Ridout and Linkie 2009).

RESULTS

We recorded 1058 independent detections of panthers, 1799 independent detections of adult (i.e. ≥1 year of age) male deer, and 2624 detections of adult female (i.e. ≥1 year of age) deer from February-October 2015. At the diel timescale, only 28% (n = 296) of panther detections occurred during diurnal periods. Spatially, 91% (n = 966) of panther detections occurred at on-trail traps. Sixty-five percent (n = 1177) of male deer detections were diurnal and 65% (n = 1175) occurred at on-trail traps. Seventy-one percent (n = 1862) of female deer detections occurred during diurnal hours while 60% (n = 1565) of adult female deer detections occurred at on-trail traps. However, only 11% (n = 279) of female deer detections occurred on-trail during nocturnal hours.

Detection rates

The most supported model for panthers and both sexes of deer included trail *x* time, trail *x* season, and season *x* time interactions (Table 2.1). We observed an interactive effect of trail and time on the rate of detection of panthers (Fig. 2.3). This interaction is evident in an 875% increase in detection rates from diurnal off-trail traps during the rut (0.24, 95% CI: 0.15-0.36; detections/1000 hours) to nocturnal on-trail traps in the fawning season (1.02, 95% CI: 0.80-1.24). We also observed a season *x* time interactive effect on detection rates of panthers with diurnal and nocturnal detection rates being highest during the fawning season at both on-trail and off-trail traps. The detection rate of panthers was greater on-trail than off-trail during both day and night across all seasons with the highest detection rates observed off-trail at night during the fawning season (1.03, 95% CI: 0.82-1.28) and on-trail at night during the rut (1.02, 95% CI: 0.80-1.24) and lowest rates of detection at off-trail traps during diurnal hours of the pre-rut (0.23, 95% CI: 0.13-0.34) and rut seasons (0.24, 95% CI: 0.15-0.36)

The difference between diurnal and nocturnal detection rates clearly identified nocturnal hours as periods of higher predation risk to deer. At the seasonal scale, panther activity varied little with the exception of increased diurnal activity during the fawning season. Spatially, panther detection rates were much higher at on-trail traps than off-trail suggesting high risk of predation in the vicinity of trails. Thus, we considered deer activity in the context of spatially and temporally variable risk of predation. We classified diurnal and nocturnal periods as low- and high-risk times, respectively, and we considered on-trail and off-trail locations as areas presenting respective high and low risk. Thus, diurnal, off-trail activity imposed the least risk and nocturnal, on-trail activity imposed the greatest risk.

For male deer, we observed significant interactive effects of trail and time as well as time and season on detection rates (Fig. 2.4). In high-risk areas at low-risk times, detection rates (detections/1000 hours) of males were lowest during the fawning season (0.98, 95% CI: 0.77-1.20) and peaked during the rut (3.31, 95% CI: 2.80-3.90). Detection rates were greater at low-risk times than high-risk times across all seasons. In high risk areas at high risk times, male activity was lowest during the fawning season (0.23, 95% CI: 0.15-0.31) and increased each season through the rut (2.09, 95% CI: 1.60-2.54) then decreased during the post-rut (0.93, 95% CI: 0.75-1.16). In low-risk areas at low-risk times, activity of males was lowest during fawning (0.90, 95% CI: 0.64-1.20) and peaked during pre-rut (2.35, 95% CI: 1.81-2.90) and rut (2.12, 95% CI: 1.64-2.76). In low-risk areas, male activity during low-risk times was greater than during high-risk times during fawning and rearing, but there was no difference during any other season.

We observed interactive effects of trail and time as well as season and time on detection rates of female deer (Fig. 2.5). Detection rates of females were greater at low-risk times across all seasons regardless of location. The greatest female detections rates occurred in high risk areas at low-risk times during the rearing (2.79, 95% CI: 2.38-3.22), pre-rut (3.23, 95% CI: 2.64-3.79), and rut (3.98, 95% CI: 3.41-4.65) seasons. However, detection rates of females at high-risk times were greater in low-risk areas through all seasons.

Activity overlap

We observed significant effects of trail and season on the coefficient of overlap of males and females with panthers (Fig. 2.6). In low-risk, off-trail areas, the sexes only differed in overlap with panthers during the fawning season when female-panther overlap was greater. However, the sexes differed in overlap with panthers during all seasons in high-risk, on-trail areas where females overlapped with panthers more during the fawning season, and male-panther overlap was greater during the rearing, pre-rut, rut, and post-rut seasons. We also observed seasonal differences in overlap within the sexes. In low-risk areas, activity overlap was greater during fawning and rearing than pre-rut, rut, and post rut for both sexes, and female-panther overlap was lower during the rut than any other season. In high-risk, on-trail areas, female-panther overlap was greatest during the fawning season while male-panther overlap was greatest during the rut. Within the sexes, we also observed effects of spatial variation in risk of predation on deer-panther overlap; female-panther overlap was lower in high-risk areas than low-risk areas during fawning and rearing while male-panther overlap in high-risk areas was lowest during rearing and greatest during rut.

DISCUSSION

Our results provide strong correlative evidence that risk of predation by panthers induces white-tailed deer activity patterns that are substantially different from activity patterns in other parts of their range where panthers do not occur. Activity patterns of deer vary based on geographical, physiological, and environmental factors, however peaks in activity during crepuscular hours are ubiquitous across the species' range (Kammermeyer and Marchinton 1977; Beier and McCullough 1990). Increases in nocturnal activity of deer exposed to human hunting pressure are also well documented (Kilgo et al. 1998; Kilpatrick and Lima 1999; Webb et al. 2010; Little et al. 2015). However, our results suggest that both sexes of deer displayed preference for diurnal activity and support the 'risky times hypothesis', which predicts that prey respond to temporal variation in risk. Our results suggest that males engaged in riskier, nocturnal activity more than females, which may be attributed to their inability to forgo activity during periods of high risk while meeting energetic requirements for maintaining reproductively competitive body mass. Conversely, female detection rates suggest a strong aversion to nocturnal activity.

In addition to sex-specific responses of deer to temporal variation in risk of predation, we also found sex-specific responses to spatial variation in risk, which support the 'risky places hypothesis'. In our study, on-trail detection rates of panthers were up to 875% higher than off-trail rates. This difference in space use by panthers allowed us to test for the effects of spatial variation in risk of predation, which revealed apparent avoidance of high-risk areas by deer, particularly at high-risk times. The ability of prey to perceive spatial variation in risk and alter their behavior accordingly has been demonstrated across taxa (Sih 1980; Brown 1999). Such behavioral decisions made under the risk of predation are the process by which the "landscape of fear" is shaped (Laundré et al. 2001). For example, Altendorf et al. (2001) demonstrated that mule deer (*O. hemionus*) sympatric with cougars (*P. c. cougar)* of western North America perceive forest edges as high-risk areas using giving-up densities. Conversely, re-introduction of wolves shifted habitat selection by elk from open habitat types to closed-canopy habitats (Creel et al. 2005).

In accordance with the reproductive strategy hypothesis, we predicted that males would be more active in high risk scenarios than females and that the sexes would be most risk prone during times of relative reproductive importance (i.e. rut and rearing for bucks and does, respectively). Predation risk is the crux of the reproductive strategy hypothesis – referred to as the predation risk hypothesis by Ruckstuhl and Neuhaus (2000) – which aims to explain sexual segregation in polygynous ungulates as an interactive function of predation risk and reproductive obligations (Main et al. 1996). Under this framework, the reproductive cycles of the sexes are associated with different energetic demands resulting in differential predisposition to high-risk behaviors. As predicted, we observed increased exposure to high-risk scenarios for male and female deer during seasons of high reproductive importance. Female detection rates during high-risk times were greatest in low-risk, off-trail areas during the fawning and rearing seasons when energetic demands are greatest due to lactation. Alternatively, our results indicate riskier male activity leading up to and during the breeding season when males seek out and compete for mates.

Data on activity overlap further supported the hypothesis that reproductive strategy explains the behavioral differences between the sexes. Female deer experience the greatest temporal overlap in activity with panthers during fawning at both on- and off-trail traps, but relatively high diurnal activity of panthers during fawning may have contributed to increased overlap. However, relatively high female overlap with panthers during the rearing season, particularly off-trail, may be explained by increased female nocturnal activity. Females experience a relatively short but intense increase in energetic demand associated with lactation, but can otherwise energetically afford the relative safety of decreased activity. Conversely, male fitness is positively correlated with body mass, which requires a greater frequency of high-risk foraging bouts.

A growing body of evidence suggests that anthropogenic disturbance may affect predator-prey systems with adverse consequences for prey populations (Stuart-smith et al. 1997; DeGregorio et al. 2014). Caribou (*Rangifer tarandus*) mortality sites associated with wolves and human hunting were closer to roads than random caribou telemetry locations (James and Stuart-Smith 2000). Our results provide strong evidence that deer on our study site perceive ORV trails as high-risk areas and reserve activity in those areas for low-risk times suggesting that ORV trails may facilitate efficient movement of panthers across the southwestern Florida landscape.

Following reintroduction of wolves to the Greater Yellowstone Ecosystem (Wyoming, USA) in the mid-1990's (Laundré et al. 2001), shifts in elk behavior, such as alterations in vigilance rates and space use, demonstrated the profound behavioral impacts predators can have on prey (Creel et al. 2005; Kauffman et al. 2007; Halofsky and Ripple 2008; Winnie 2012). Our results afford the unique opportunity for comparison of post-restoration behavioral effects of canid versus feline predators on North American cervid species. Unlike Creel et al. (2008), who provided support for the 'risky places hypothesis', but found none for the 'risky times hypothesis', our results support both. These differences in findings may be a function of predator hunting mode. Ambush predators, such as panthers, should exact greater non-consumptive effects than cursorial predators, as there likely are habitat cues associated with ambush predators while encounters with cursorial predators are less predictable (Preisser et al. 2007). Although our study lacks the design to causally link panthers to spatiotemporal shifts in deer activity, we suggest future research focus on comparing deer activity in the presence and absence of predators to further develop our understanding of the impacts of predator hunting mode on prevalence and relative magnitude of behavioral risk effects. Our results provide support for the hypothesis that predation risk shapes the spatial distribution and temporal activity patterns of prey populations (Brown et al. 1999; Laundré 2010) as well as evidence that white-tailed deer perceive spatial and temporal variability in risk and alter their behavior to mitigate exposure to that risk.

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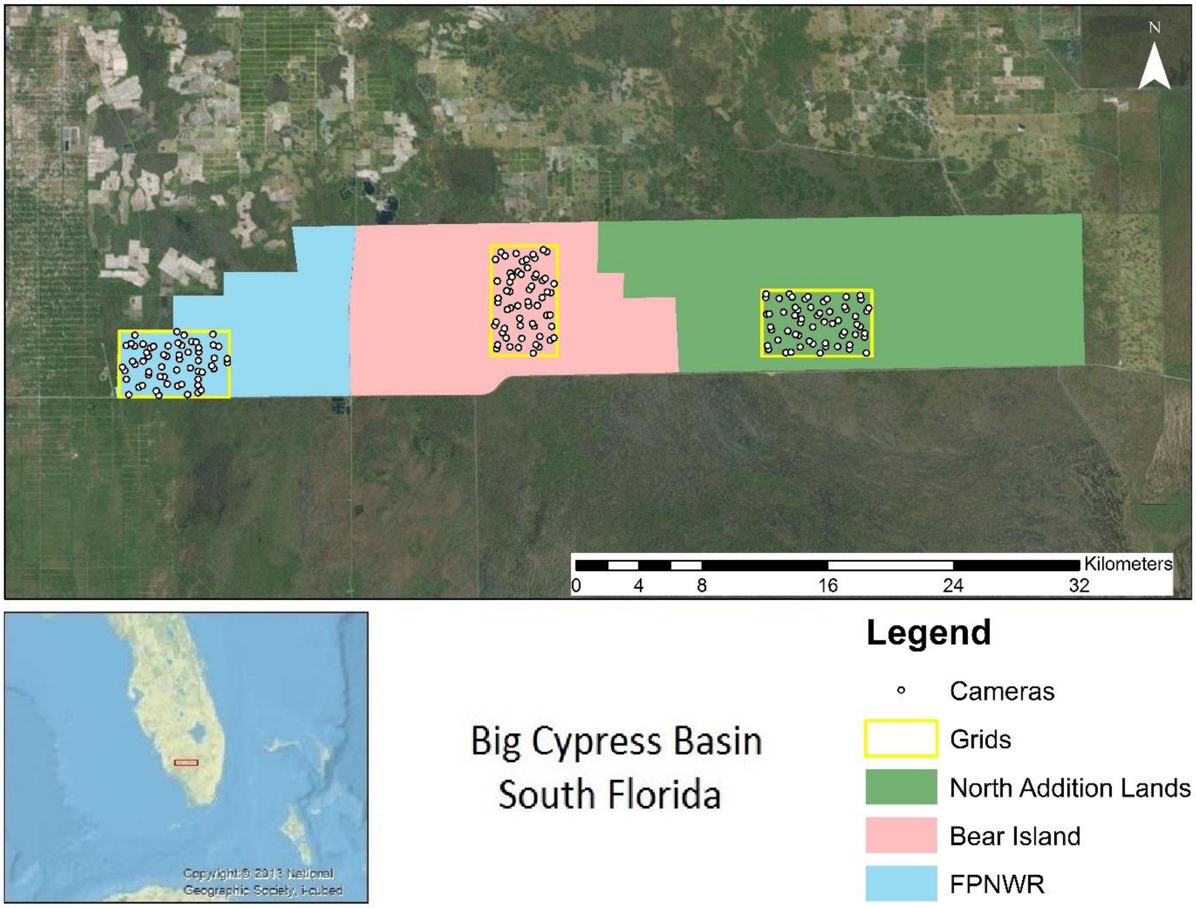

Figure 2.1. The research site was located in the Big Cypress Basin of southwestern Florida. To estimate the effects of risk of predation by Florida panthers on white-tailed deer behavior, we deployed 60 infrared-triggered cameras in each of 3 grids. Grids were separated by ≥ 13 km and were located in the Florida Panther National Wildlife Refuge and the Bear Island and North Addition Lands units of the Big Cypress National Preserve

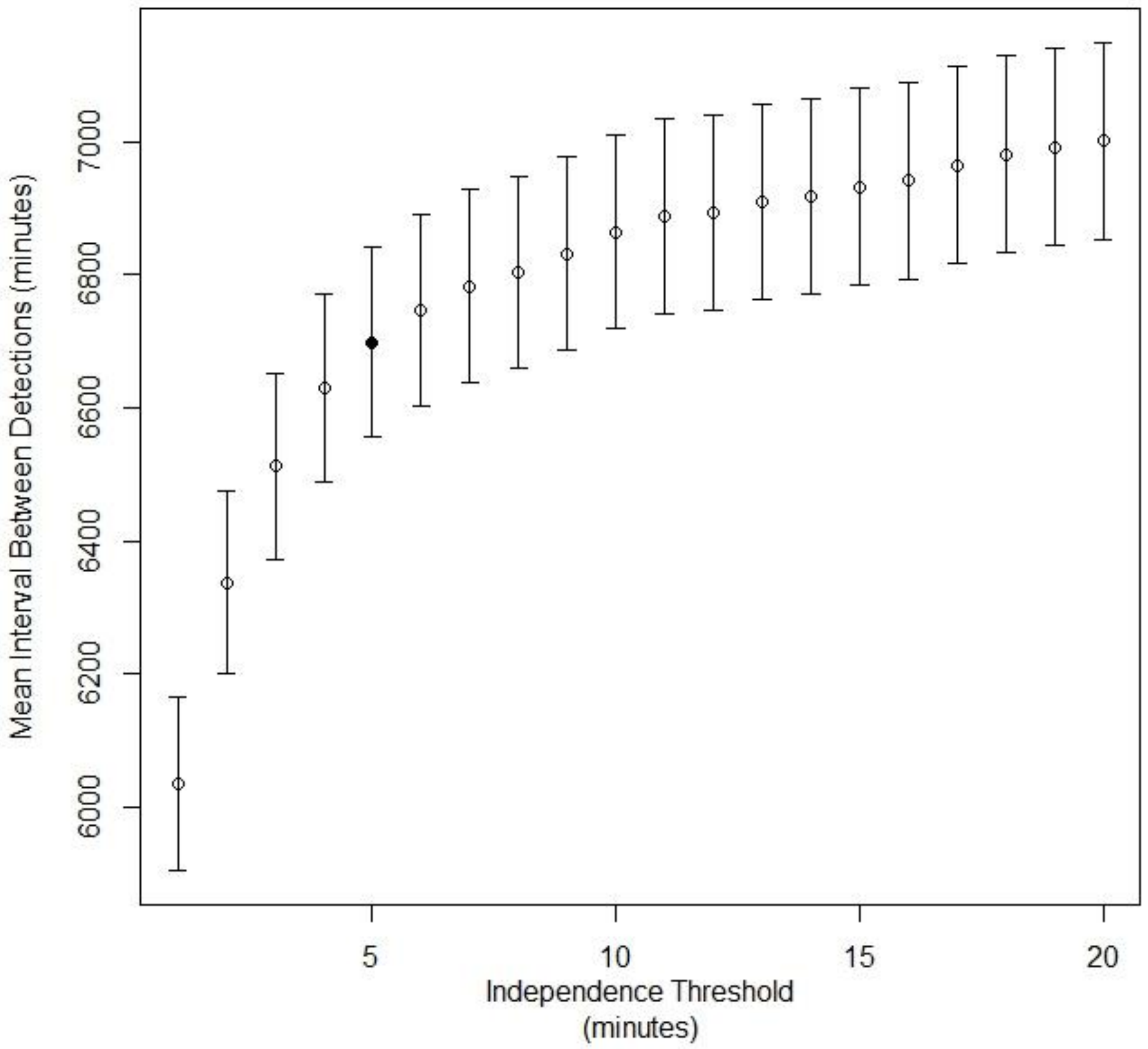

Figure 2.2. To maximize independence of detections, we sorted images chronologically by camera and systematically filtered images at one minute intervals taking the mean interval between detections for each resulting dataset. A marked decrease in the rate of change in mean interval upon ommission of detections occuring ≤ 5 minutes appart indicated sufficient independence of detections at that threshold.

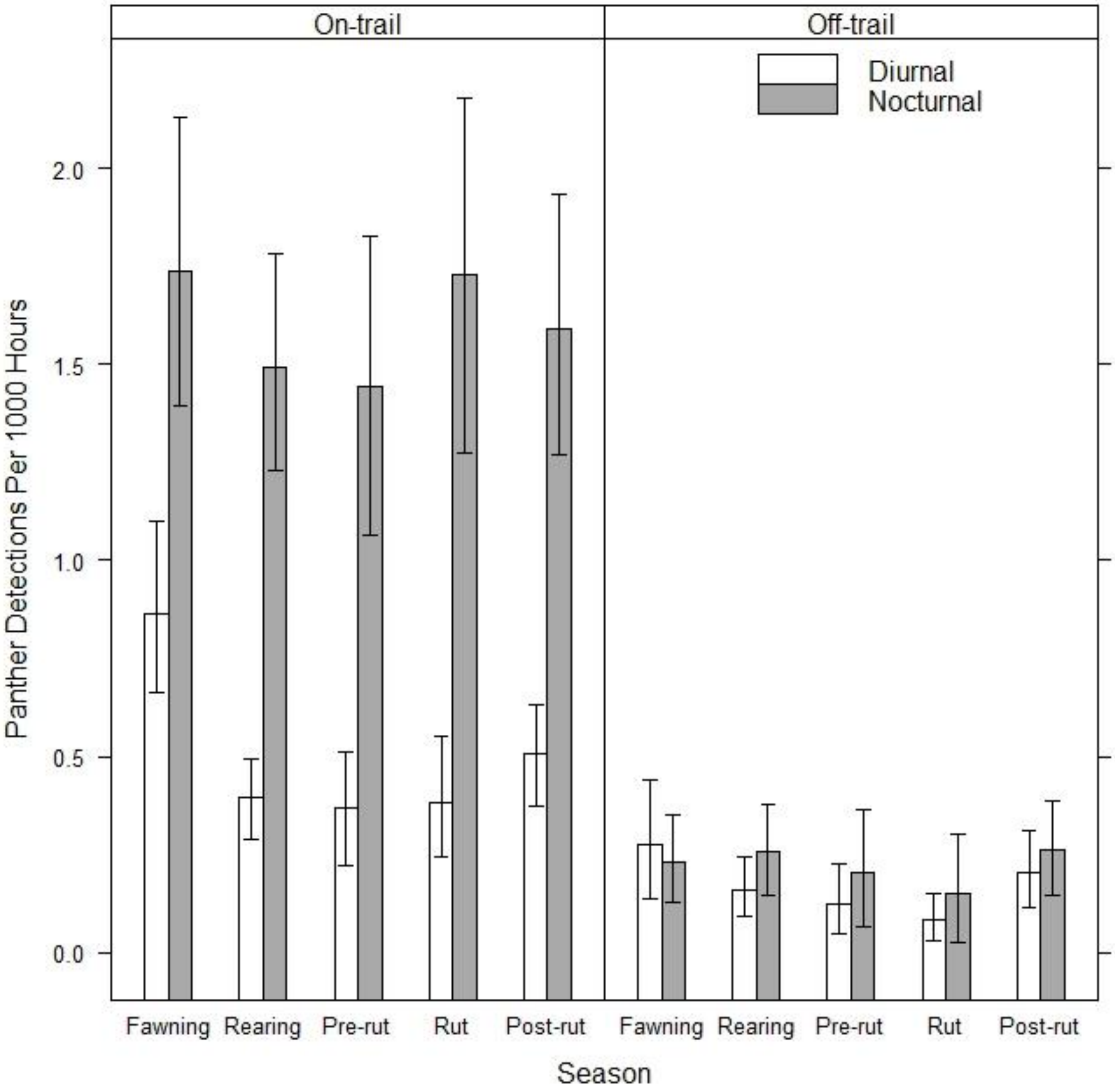

Figure 2.3. Diurnal and nocturnal panther detections per 1000 hours at on- and off-trail camera traps by biological season, Big Cypress Basin, Florida. Fawning includes February-March 2015, rearing includes April-June 2015, pre-rut includes July 2015, rut includes August 2015, and post-rut includes September-October 2015. Error bars indicate bootstrapped 95% confidence intervals.

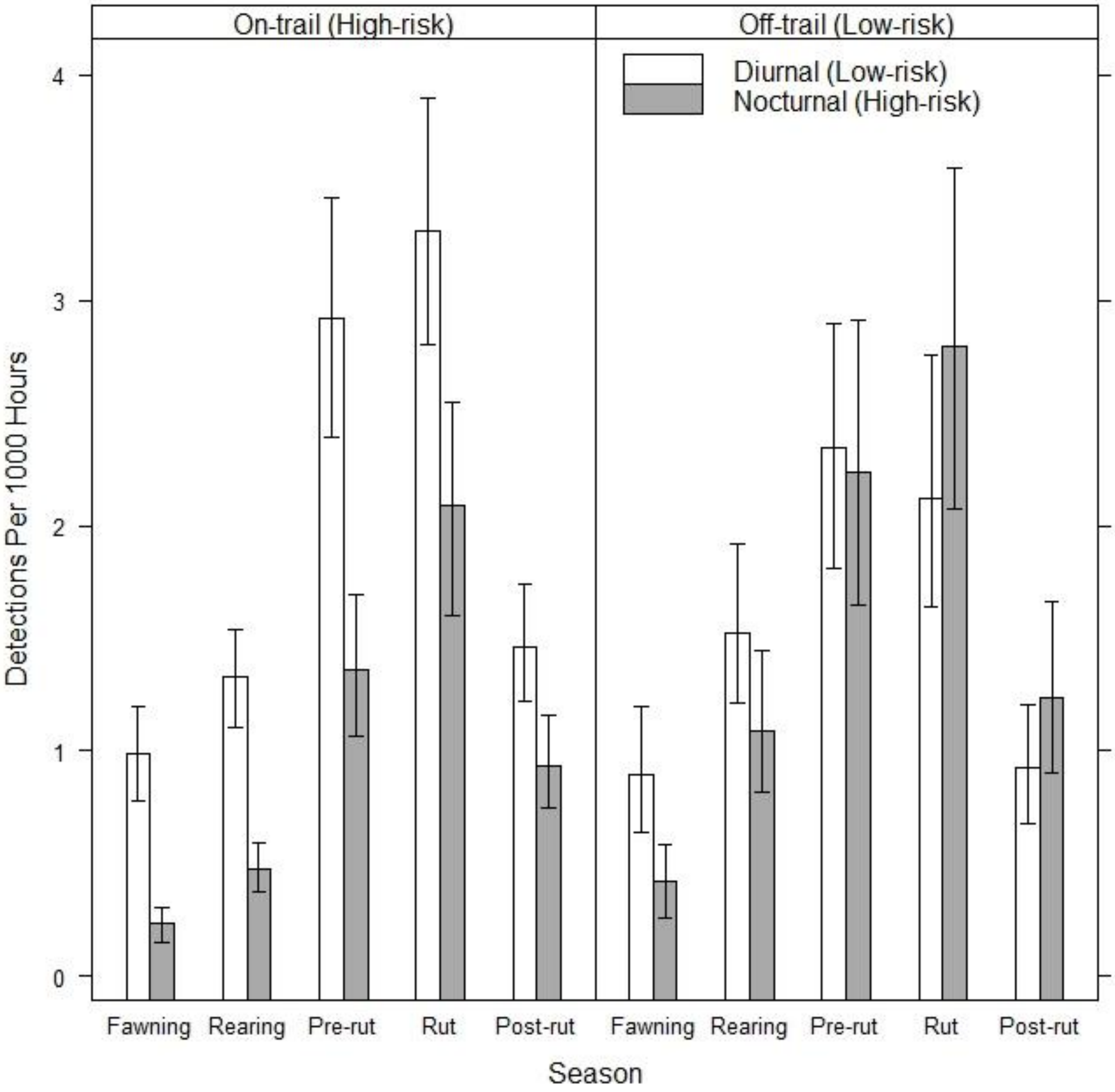

Figure 2.4. Diurnal and nocturnal male deer detections per 1000 hours at on- and off-trail camera traps by biological season, Big Cypress Basin, Florida. Fawning includes February-March 2015, rearing includes April-June 2015, pre-rut includes July 2015, rut includes August 2015, and post-rut includes September-October 2015. Error bars indicate bootstrapped 95% confidence intervals.

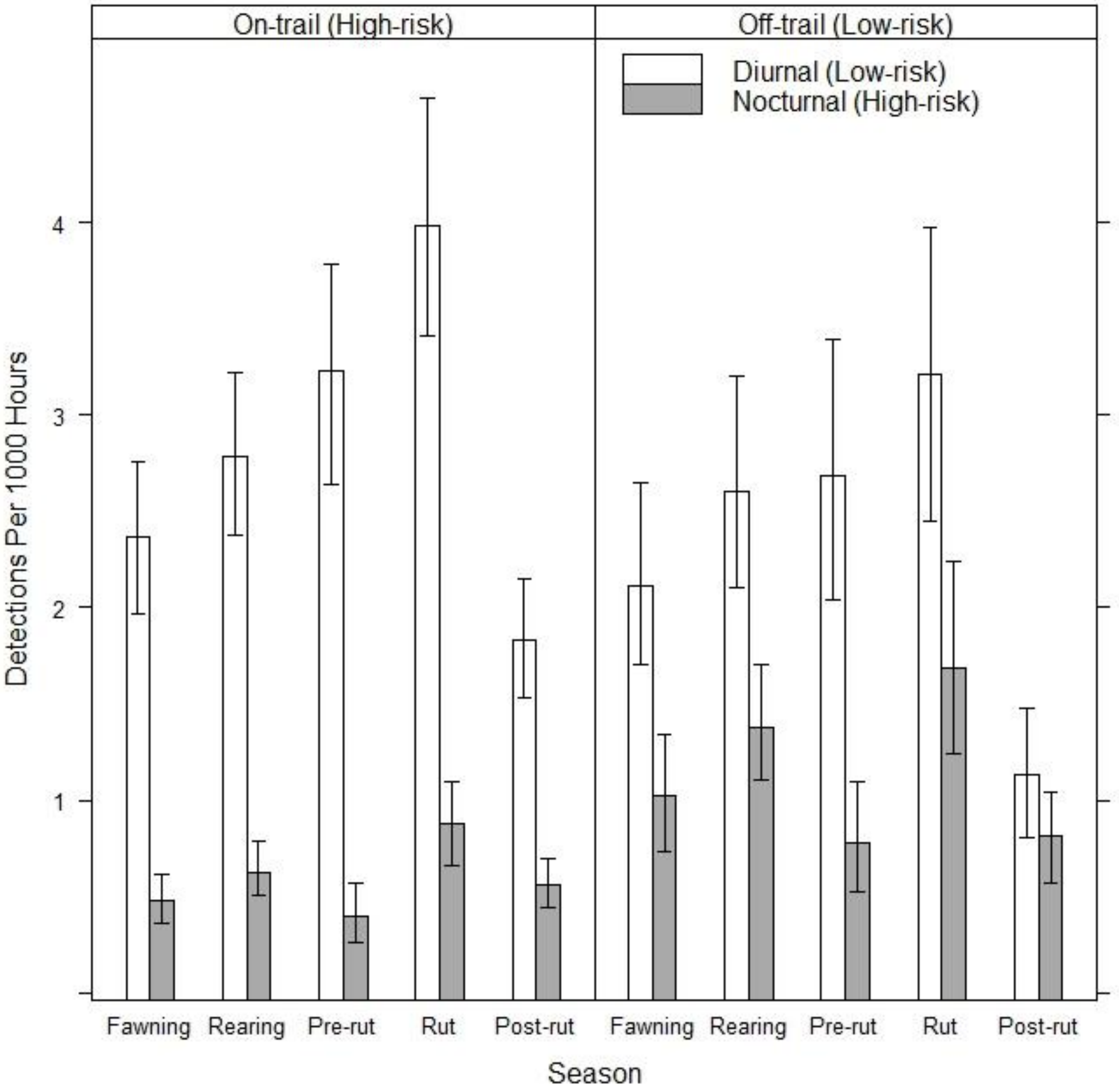

Figure 2.5. Diurnal and nocturnal female deer detections per 1000 hours at on- and off-trail camera traps by biological season, Big Cypress Basin, Florida. Fawning includes February-March 2015, rearing includes April-June 2015, pre-rut includes July 2015, rut includes August 2015, and post-rut includes September-October 2015. Error bars indicate bootstrapped 95% confidence intervals.

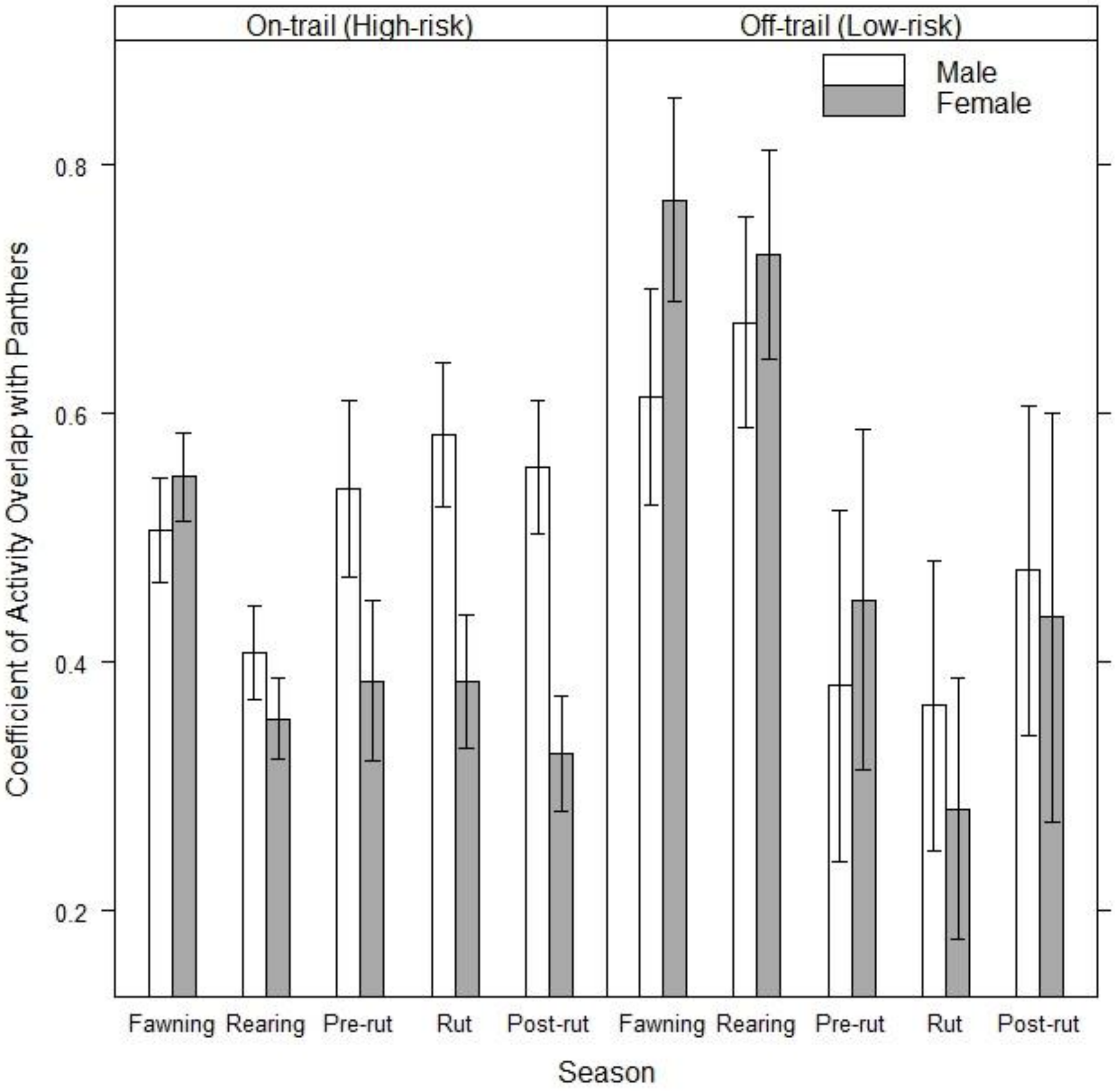

Figure 2.6. Overlap of male and female deer activity patterns with panther activity at on- and off-trail camera traps by biological season, Big Cypress Basin, Florida. Fawning includes February-March 2015, rearing includes April-June 2015, pre-rut includes July 2015, rut includes August 2015, and post-rut includes September-October 2015. Error bars indicate bootstrapped 95% confidence intervals.

Table 2.1. Model selection results for models used to predict for male and female (≥6 months old) white-tailed deer at camera traps on the Big Cypress National Preserve and Florida Panther National Wildlife Refuge in Collier County, FL, USA (February-October 2015).

Model	**Parameters**	**AICc**	**ΔAICc**	**AICc Weight**
Male Deer				
Trail:Season + Trail:Time + Season:Time	17	12601	0	1
Season:Time	11	12803	202	0
Trail:Time + Season	9	12926	325	0
Trail + Season + Time	8	12935	335	0
Female Deer				
Trail:Season + Trail:Time + Season:Time	17	16116	0	1
Trail:Time + Season	9	16512	396	0
Season:Time	11	16943	826	0
Trail + Season + Time	8	17004	888	0
Panther				
Trail:Season + Trail:Time + Season:Time	17	5307	0	1
Trail:Time + Season	9	5354	47	0
Trail + Season + Time	8	5384	77	0
Season:Time	11	5410	103	0

CHAPTER 3

EFFECTS OF HYDROLOGY AND PREDATION ON THE SPATIAL ECOLOGY OF WHITE-TAILED DEER IN THE BIG CYPRESS BASIN OF FLORIDA [1]

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[1] Crawford, D.A., M.J. Cherry, B.D. Kelly, E.P. Garrison, D.A. Shindle, L.M. Conner, R.B. Chandler, and K.V. Miller. To be submitted to the *Journal of Wildlife Management*

ABSTRACT

Home range size and resource selection of white-tailed deer (*Odocoileus virginianus*) are influenced by region-specific biotic and abiotic factors. In the Big Cypress Basin (BCB) of southwestern Florida, deer must negotiate risk of predation and temporal variability in resource availability, which results from seasonal inundation. The reproductive-strategy hypothesis states that different energetic demands associated with reproduction should result in different resource selection by males and females outside of the breeding season. Risk of predation further influences differences in resource selection as females should select the safest habitat for rearing offspring with adequate, if suboptimal, energetic resources. Recent shifts in the predator community and reported declines in regional deer populations warrant investigation of the spatial ecology of the BCB deer herd. We assessed resource selection and home range size of deer in the BCB and interpret results in the context of reproductive demands and spatiotemporally variable risk of predation and resource availability. Both sexes avoided presumably high-risk edges during dry periods, especially at high risk times, however as open canopy habitats became inundated, selection for edges increased. Similarly, females selected for marshes during the dry 2015 fawning season but avoided marshes during the wet 2016 fawning season when males showed no selection. Furthermore, home range size and core area were positively correlated with water depth for both sexes, however the extent to which male space use increased was greater than that of females. Our results provide support for the reproductive-strategy hypothesis and suggest that predation risk may drive sex-specific variation in resource selection. However, when flooding limits resource availability, sex-specific differences erode as risk of starvation takes priority over risk of predation in the context of behavioral decision-making.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*; hereafter, deer) habitat selection and home range size are influenced by various factors including population demographics, local climate, forage abundance, social behavior, and disturbance (Stewart et al. 2011). Home ranges of deer can differ in size and habitat composition as various biological factors often incur different resource demands and changing habitat conditions affect resource availability. For example, female home ranges are constricted immediately before and for up to 2 months after parturition (Ozoga et al. 1982) when energetic demand for lactating females peaks and safety for vulnerable offspring is at a premium. Small spring and summer male home range sizes are attributed to increased forage availability during respective growing seasons (Nelson and Mech 1981, Beier and McCullough 1990, Olson 2010). Age-specific processes, such as natal dispersal, may also affects space use (Downing et al. 1969, Kammermeyer and Marchinton 1976, Long and Diefenbach 2005, McCoy et al. 2005, Long et al. 2008, Nelson and Mech 2008). However some facets of deer movement remain unexplained (Kolodzinski et al. 2010, Karns et al. 2011, Olson et al. 2015, Jacobsen 2017). Understanding temporal variability in space use and habitat selection of individuals and across demographic groups is needed to determine the relative importance of resources to animals.

Across their range, resource availability plays a major role in determining when and where deer choose to spend time as environmental conditions cause variation in the availability of resources. For example, at higher latitudes, deer often seek refuge from harsh winter conditions in dense evergreen thickets that provide thermal cover, relative safety from predators, and meager forage (Messier and Barrette 1985). Conversely, deer in southwestern North America often seek shelter from solar radiation during summer months (Ockenfels and Brooks

1994). In the Big Cypress Basin of southwestern Florida, deer experience seasonal variation in resource availability as a result of widespread seasonal flooding. In this region, approximately 65% of annual precipitation occurs during summer months, typically inundating a majority of the landscape for prolonged periods (Duever 1986). However, drought conditions are not uncommon in winter months resulting in pronounced wet and dry periods that are highly variable in terms of timing, intensity and duration. Despite variable timing, the wet and dry seasons are typically considered from May 1-October 31 and November 1-April 30, respectively. This seasonal hydrology affects many aspects of white-tailed deer ecology in southern Florida, including breeding chronology and spatial-use. Annual variation in hydrology can have profound influences on deer demography and habitat selection (Richter and Labisky 1985, Miller 1993, Labisky and Boulay 1998, Labisky et al. 1999, MacDonald-Beyers and Labisky 2005). For example, Sargent (1992) and Miller (1993) found no effect of standing water on deer movement contrary to the conclusions of Flemming et al. (2005) and Loveless (1959*a*). However, Sargent (1992) and Miller (1993) collected data in years of relatively low precipitation with mean water levels not exceeding 0.3 m. MacDonald-Beyers and Labisky (2005) compared years of relatively high and low standing water and documented significant shifts in habitat selection and a 100% increase in mortality rates of radio-collared deer in 1994-1995, a year of record high water (mean water level = 0.73 m). Specifically, they observed strong selection for hardwood hammock “islands”, which remained relatively dry. Use of GPS-telemetry and evolving analytical techniques present opportunities to gather and analyze fine-scale spatiotemporal data necessary to evaluate habitat-specific effects of seasonal flooding on selection and home range size of deer.

While seasonal inundation may affect space use at a broad temporal scale, risk of predation must be continuously assessed by prey species as they make behavioral decisions about when and where to forage in the context of spatiotemporal variability in risk. Predators directly affect prey populations by removing individuals from the population and indirectly by inducing morphological, physiological, and behavioral shifts in response to the risk of predation (McCollum and Leimberger 1997, Brown 1999, Clinchy et al. 2013). Prey behaviorally mitigate risk by changing rates of vigilance, patterns of activity, or space use. While mortality of white-tailed deer attributed to direct predation has been well documented in the south Florida system (Beier and McCullough 1990, Land 1991, Miller 1993, Labisky and Boulay 1998, Beier et al. 2003), these studies occurred prior to or shortly after the genetic restoration of the endangered Florida panther (*Puma concolor coryi*). In 1995, 8 wild-caught female puma from Texas were released in southern Florida for genetic introgression purposes. Since that time, the panther population has increased 600%, from 20-30 individuals to a minimum of 130 adults. How the increase in panther abundance affects deer in terms of both direct and indirect effects is unknown. Furthermore, evidence suggests the indirect effects of a predator may be predicted by the hunting mode of the predator (Lingle 2001, Lingle and Wilson 2001, Stankowich and Coss 2007). Sit and pursue and ambush predators such as panthers may have greater non-consumptive effects on their prey than wide-ranging cursorial predators because informative habitat cues (e.g., edge) can be associated with risk (Schmitz 2008). To date, no studies have addressed the indirect effects of predation on deer in the Florida panther range, particularly as related to habitat selection. The coupled effects of hydrology and increased predation risk may drive habitat selection and avoidance patterns of white-tailed deer in southern Florida.

We examined sex-specific home range size and habitat selection of white-tailed deer in Florida's Big Cypress Basin at diel and seasonal time scales in the context of predation risk, hydrology, and reproductive biological processes. In accordance with the reproductive-strategy hypothesis (Main et al. 1996), we hypothesized that male and female home range size and habitat selection would differ due to differing reproductive requirements. We predicted that male deer would have larger home ranges and core areas than females and that sex-specific habitat selection would diverge most during the fawning and fawn rearing seasons. We hypothesized that water levels would affect home range size and resource selection and predicted that high water levels would increase home range size and selection of drier habitat types for both sexes. We tested the hypothesis that deer would avoid spatial features associated with relatively high risk of predation ("risky places hypothesis"), particularly at high-risk times ("risky times hypothesis"). We considered forest edge and off-road vehicle (ORV) trails to be associated with relatively high risk of predation by panthers and nocturnal hours to be high-risk times as forest edges provide concealment cover for panthers and ORV trails and nocturnal hours are preferred corridors and activity times of panthers, respectively (Crawford, D.A., *unpublished data*). We predicted that use of high-risk areas would be positively correlated with surface water levels as increased water depth decreases availability of otherwise preferred resources. Lastly, we hypothesized that selection for high-risk features at high-risk times would increase during the breeding season when individuals may be forced to forgo safety to meet the demands of reproduction. Consistent with this hypothesis, we predicted that nocturnal selection for roads and forest edges would increase during the fawn-rearing season and breeding season for females and males, respectively.

METHODS

Study Site

We conducted our research in the Big Cypress Basin (BCB) of southwestern Florida. A subtropical climate and minimal relief strongly influence the distribution of vegetation communities across the landscape resulting in a heterogeneous mosaic of open and closed-canopy habitat types (Duever 1986). While annual precipitation ranges from 114-127 cm (Obeysekera et al. 1999), tropical and convective storms in this region typical of summer months account for more than 60% of annual rainfall while the mild winters are relatively dry resulting in distinct wet and dry seasons (Hela 1952). Furthermore, local precipitation patterns largely depend on broad scale maritime wind and ocean current patterns resulting in significant annual variability in time and duration of the wet season. Potential evapotranspiration reportedly accounts for 70-90% of surface water removal, which peaks in the spring (Duever et al. 1994). Average daily temperatures range from 17° C to 25° C with mean maximum daily temperatures ranging from 22-30º C (Obeysekera et al. 1999). From March to December, temperatures consistently exceed 27º C while temperatures above 25º C are common even through the winter.

Regional topography is characterized by minimal relief with slight ridges delineating relatively flat basins interspersed with depressions that retain standing water throughout the dry season (Loveless 1959b; Duever 1986). A 9 cm/km slope to the southwest induces a southwestern sheet flow of water across the landscape. Low relief along with warm season precipitation characteristic of the regional climate contribute to seasonal inundation of much of the landscape with mean water depths ranging from 0.3-0.73 m (Duever 1986).

The unique hydrological cycle of the BCB largely shapes local vegetation communities. Five vegetation communities, including pine flatwoods, hammock forests, cypress forests, prairies, and marshes, dominate the Big Cypress Basin (McPherson 1974). Pine flatwoods indicate relatively dry sites consisting of slash pine (*Pinus elliottii*) with an understory dominated by saw palmetto (*Serenoa repens*). Hardwood shrubs such as black titi (*Cliftonia monophylla*), gallberry (*Ilex glabra*) and wax myrtle (*Morella cerifera*) are found where saw palmetto is less dense while woody vines such as poison ivy (*Toxicodendron radicans*) and greenbrier (*Smilax* spp.) grow throughout the understory (Harlow 1959, McPherson 1974). Harlow (Harlow 1959) attributed relatively high quantities of forbs in flatwoods of southern Florida, such as vanilla plant (*Trilisa odoratissima*) and erect spadeleaf (*Centella erecta*), to a mild climate. Pine flatwoods tend to remain dry throughout the year only experiencing inundation in extreme high-water events.

Hydric hardwood hammocks occur on limestone ridges found interspersed among swamps and flatwood communities of the region and, while they have poorly drained soils, they are rarely, if ever, inundated (McPherson 1974). The overstory of hammocks are dominated by hardwoods such as live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*), which can grow in pure stands. Broad-leaved tropical species such as strangler fig (*Ficus aurea*) and gumbo limbo (*Bursera simaruba*) are more common in southern portions of the study site. Hammocks vary in understory composition and density depending on density of overstory species. Dense hammocks of cabbage palm result in a sparse understory of woody vines while more open stands of oak and cabbage palm give rise to shrubs such as black titi and wax myrtle.

We aggregated several cypress-dominated communities into a single cypress class. Dwarf cypress (*Taxodium distichum*) forests occur in relatively thin stands of stunted trees with an herbaceous understory of grasses (e.g., *Cladium mariscus*) and rushes (*Juncus* spp.). Cypress domes occur in small, circular or ovoid depressions with taller trees growing in the center where soils are deepest, thus resulting in a domed appearance on the horizon (Brown 1981). Cypress is the dominant overstory while water tupelo (*Nyssa biflora*) dominates the midstory with Virginia chain fern (*Woodwardia virginica*) and panic grasses (*Panicum* spp.) as the dominant ground cover. The peripheral understory of domes is similar to that of dwarf cypress stands, however decreased elevation toward the center of domes can result in openings containing emergent wetland vegetation such as pickerelweed (*Pontederia lanceolata*) and alligator flag (*Thalia geniculata*). Cypress strands are large, north-south oriented expanses of mixed cypress swamps with dense tangles of cypress and hydric hardwood trees and shrubs (e.g., *I. glabra*, *Persea palustris*), woody vines (e.g., *T. radicans*, *Smilax* spp.), and epiphytes (*Tillandsia fasciculata*), and are indicative drainages (Harlow 1959, Brown 1981).

Marshes are characterized by emergent wetland vegetation such as sawgrass (*Cladium mariscus*) and rushes (*Juncus* spp.) with alligator flag (*Thalia geniculata*) dominating deeper depressions. Dense, monospecific willow heads (*Salix caroliniana*) and pop ash (*Fraxinus caroliniana*) thickets commonly occur on the periphery of deep depressions. Typical water depths in marshes are several centimeters deeper than surrounding wet prairies and swamps (McPherson 1974). Marshes, wet prairies, and cypress communities are the first to flood during the wet season and the last to dry while dry prairies only experience inundation for brief periods during peak surface water levels. Because of similarities in hydroperiod, we included wet prairies in our classification of marshes as wet prairies are dominated by grasses near their periphery but are centrally dominated by marsh plant communities, primarily sawgrass and alligator flag. Our classification of prairies included only the dry variety, which are dominated by grasses such as *Panicum* spp. and low shrubs such as wax myrtle with few trees.

We conducted our research on the adjacent Florida Panther National Wildlife Refuge and Big Cypress National Preserve (henceforth, FPNWR and BCNP, respectively). Within BCNP, research occurred on two management units, the Bear Island (BI) unit and Northeast Addition Lands (AL) unit. All three sites lie north of I-75, a divided highway between Naples and Miami with FPNWR separated from BI by the two-lane highway, S.R. 29. To the east of S.R. 29, BI separates FPNWR and AL, the westernmost study site. The FPNWR consisted of approximately 100 km^2 and contained the highest and lowest off-road vehicle (ORV) trail and edge densities, respectively. The extensive ORV trail network facilitates frequent prescribed burning conducted for habitat management, although public access was prohibited. The FPNWR is dominated by cypress strands (~59%) and pine flatwoods (~18%) with minimal representation of prairie (~12%), hammock (~8%), and marsh (~3%) communities. Bear Island consisted of approximately 190 km^2, permitted year-round public access, allowed use of ORVs on designated trails, and permitted deer hunting from the first Saturday in September through the first weekend in January. ORV trail density and edge density were lowest and highest, respectively, in BI. Bear Island is dominated by marsh (~35%) and cypress (~32%) communities with interspersed flatwoods (~19%), hammock (~8%), and dry prairie (~4%) communities. Lastly, AL consisted of approximately 271 km^2 accessible to the public at all times, and experienced hunting pressure from September 5 through the first weekend in January. However, access to AL was walk-in only, and limited issuance of hunting permits ensured minimal hunter densities. While AL was only publicly accessible to pedestrian traffic, an ORV trail network was maintained to facilitate administrative access for research and wildfire response efforts. Cypress communities (~52%) dominated AL with flatwoods (~20%) being the second most prevalent habitat type followed by marshes (~11%), hammock (~8%), and dry prairies (~7%). The AL unit contained intermediate

ORV trail and edge densities relative to the other two sites. The sites also represented a hydrological gradient as mean surface water depth increased moving east across the sites such that the western most site, FPNWR experienced less extreme inundation for a shorter duration than the easternmost, AL.

Study Species

Because resource selection and home range size of white-tailed deer is often linked to reproductive stage, we organized our study in the context of biological seasons of deer in the BCB (Richter and Labisky 1985). Peak breeding occurs in mid to late-August; however, the asynchronous breeding characteristic of low-latitude deer herds results in a prolonged parturition period (Richter and Labisky 1985). Concurrent camera trap data indicated a broad window of fawning across most of February and March (Engebretsen, K. N., *unpublished data*), thus we designated these months as the fawning season. This timescale was chosen to encompass periparturient and postparturient periods, and include the time period over which the majority of fawns were born. Because most fawns were born by the end of March and bucks had initiated antler growth by this point, we designated April through June as the fawn-rearing and antler growth season (hereafter rearing). This period is energetically demanding for reproductive females as lactation peaks (Moen 1978, Pekins et al. 1998). Similarly, males experience nutritional demands of antler development and body growth. We designated July as the pre-rut when males exhibit hyperphagy, increased activity, and increased antler sparring in preparation for conspecific competition. The breeding season occurs throughout August and is a stressful time for males as they forage minimally and maximize mate searching behaviors. Following the rut, males enter a recuperation phase known as the post-rut, which occurred during September and October. We designated November, December, and January as gestation throughout which bred females experience increasing energetic demands as a result of pregnancy.

Capture

From 04 January 2015 to 05 May 2016, we captured 234 adult deer (*n* = 90 males; *n* = 144 females) aerially as described by Barrett et al. (1982), via chemical immobilization, or via rocket-netting (Hawkins et al. 1968). Upon capture, all deer were blindfolded. We estimated animal age using tooth wear and replacement (Severinghaus 1949). We ear-tagged each individual with a unique identifier and fit individuals ≥ 1 year old with an ATS Model G2110E GPS-telemetry collar (Advanced Telemetry Systems, Isante, MN). We programmed collars to record and store one location every 4 hours with the exception of every 5th day when a 3 hour interval enabled a rotating schedule such that each hour of the day was represented every 5 days. All data were stored on board the unit, uploaded to the ATS Server via Iridium satellite (Iridium Communications Inc., McLean, VA), and were remotely accessible. All deer were captured under University of Georgia IACUC permit A2014 07-009-Y3-A1 and in accordance with American Society of Mammalogists Guidelines (Sikes et al. 2011).

Data

From February 2015 through January 2017, we recorded 420,713 locations (*n* = 117,259 male; *n* = 303,454 female). We excluded the first two weeks of GPS data collected post capture for each individual to mitigate the influence of capture on space use. We classified locations as diurnal (occurring between sunrise and sunset) and nocturnal (occurring between sunset and sunrise) using package maptools in program R, which utilizes location coordinates to calculate accurate, site-specific sunrise and sunset times. We parsed data by month and diel time period for estimation of selection coefficients resulting in 48 data sets (e.g., diurnal and nocturnal locations during February 2015; Table 3.1). According to Burt (Burt 1943), extra-home range excursions do not characterize the home range, and such behaviors are deserving of independent consideration. Therefore, we omitted all data of all individuals engaging in such behavior from analyses. We deemed individuals with > 20 records that were ≥ 5 standard deviations farther than their mean distance to home range center ($n = 9$) as excursive individuals and, thus excluded them from analysis. We included only individuals surviving the entirety of a given month.

We reclassified rasterized habitat data (Stys et al. 2004) to the five dominant vegetation communities for use in resource selection and home range analyses. Because wet prairies often include marsh vegetation, we grouped the two. Therefore, our classification of prairie habitats included only dry prairies. Using ArcGIS 10.4 (ESRI Software, Redlands, CA, USA), we manually digitized ORV trails at a scale of 1:5000 m using aerial imagery (ESRI Software, Redlands, CA, USA; 2015). We created a polyline feature representing the boundary of open and closed canopy habitats, or edge, by dissolving all closed canopy patches into a single feature. We then created Euclidean distance rasters for each habitat type, ORV trails, and edges for use as predictor variables in distance-based hierarchical point process models of resource selection (Conner et al. 2003). We employed a distance-based approach to resource selection to mitigate telemetry error, allow for treatment of use as a continuous variable, and enable inclusion of linear features that may rarely, if ever, be used under a binary, compositional framework.

Five on-site hydrological stations maintained by the Everglades Depth Estimation Network (EDEN) project and the US Geological Survey in BI and AL recorded daily mean water depths. We averaged daily mean water depths for each month during the study. Because stations only represented hydric habitat, we used mean monthly surface water level as a relative index of inundation.

Analyses

Estimation of selection coefficients and home range size

We employed a two-stage approach to estimate the effects of sex, age, biological season, time, and mean surface water depth on resource selection by deer. We first obtained individual selection coefficients by modeling resource selection during each month using a point process model with individual-specific random effects (Hooten et al. 2017; Johnson et al. 2013). Point process models are useful for drawing inferences about the effects of environmental variables on the distribution of points, which in this case are the telemetry locations for each individual. Specifically, let $\mathbf{u}_{ik}$ denote the two-dimensional Cartesian coordinates of telemetry location k for individual i. An inhomogeneous point process models assumes that the points arise from a probability distribution that depends on the intensity function $\lambda(\mathbf{u})$, which is defined as the expected number of points in the infinitesimally small area at location $\mathbf{u}$. The intensity function must be positive, and it is therefore often modeled as a log-linear function of environmental variables. If the number of observed points (K_i) is fixed by design, as in the case of telemetry studies, the model for location k is an inhomogeneous binomial point process with probability distribution:

$$p(u_{ik}) = \frac{\lambda(\mathbf{u}_{ik})}{\int_{S_i} \lambda(\mathbf{u}) d\mathbf{u}}$$

where S_i is the two-dimensional spatial region that contains the home range of individual i (Royle et al. 2014). Spatially referenced environmental variables are never represented in continuous space, but are usually represented on a grid with a prescribed resolution and extent. In this case, $\mathbf{u}$ can be defined as the grid cell identity, rather than as a point in space, and the point process model can be approximated using a multinomial distribution (Royle et al 2013) for the number of points (n_{ij}) occurring in each of the J_i pixels within the spatial region S_i:

$$\{\mathrm{n}_{i1}, \dots, n_{iJ_i}\} \sim \text{Multinomial}(K_i, \{\pi_{i1}, \dots, \pi_{iJ_i}\})$$

The multinomial cell probabilities are given by

$$\pi_{ij} = \frac{\lambda(\mathbf{u}_{ij})}{\sum_{j=1}^{J_i} \lambda(\mathbf{u}_{ij})}$$

This model is very similar to the discrete choice model described by McCracken and Manly (1998), and it assumes that the points are independent of one another, conditional on the parameters of the intensity function. The independence assumption could be relaxed by including an explicit movement model to describe how an individual's location at time k depends on previous locations. However, such an approach would be very computationally demanding and fine-scale movement behavior was beyond the scope of this paper.

We modeled the point process intensity as a log-linear function of environmental variables and the distance to each individual's home range center:

$$\lambda(u_{ij}) = e^{\boldsymbol{x}(\mathbf{u}_{ij})\boldsymbol{\beta}_i}$$

where $\boldsymbol{x}(\mathbf{u}_{ij})$ is an L-dimensional vector of habitat variable (i.e., covariates) at grid cell $\mathbf{u}_{ij}$, and $\boldsymbol{\beta}_i = (\beta_{i1},\beta_{i2},\beta_{i3},\dots,\beta_{iL})'$ is a vector of parameters for animal *i*. We expected that selection coefficients would vary among individuals, and so we modeled the coefficients as random effects: $\beta_{iL} \sim \mathrm{N}(\overline{\beta_l},\sigma_L^2)$, where $\overline{\beta_l}$ represents the common, population-level coefficient of parameter *l* ($l = 1, 2, \dots, \mathrm{L}$). If the 95% credible interval of a given β-parameter includes 0, then there is little evidence of selection of that habitat variable. Habitat variables included distance to prairie, marsh, cypress, flatwoods, and hammock habitat types as well as distance to ORV trail and closed canopy edge. Distance to home range center at each pixel was computed by using the empirical average of the telemetry locations as the home range center (s_i). Including distance to home range center in the model served several purposes. First, it allowed us to estimate the availability of resources rather than arbitrarily prescribe availability. This can be seen by decomposing our intensity function into: $\lambda(u) = f\left(u_{ij}\right)g(u_{ij})$ where $f(u_{ij})$ is the log-linear model of environmental effects and $g\left(u_{ij}\right) = e^{-\beta_L dist(s,u_{ij})}$, the negative exponential model for availability. As β_L increases, home range decreases and resources farther from the home range center have a lower probability of being used. Secondly, including distance to home range center made it possible to simultaneously estimate selection coefficients, utilization distributions, and home range sizes. The utilization distribution is given by $\pi(u_{ij})$ and home range size can be computed as the area associated with a chosen percentile (e.g., 50% or 95%) of the cumulative distribution function. We used Bayesian inference and vague uniform priors. We sampled posterior distributions using 3 Markov chain Monte Carlo (MCMC) chains run for 5000 iterations (Smith and Roberts 1993). We assessed model convergence by visually inspecting Markov chains (Thomas et al. 2006).

Second-stage analysis of selection coefficients and home range size

Due to computational expense associated with modeling spatial, temporal, and individual-level covariates on selection coefficients, we employed a two-stage approach to estimate these effects on selection coefficients. Specifically, we assessed the effects of age, sex, biological season, hydrology, study site, and diel time period (diurnal vs. nocturnal) on selection of habitat variables. We also assessed the effects of these covariates on home range size, and core area size.

With the resulting individual selection coefficients from the previously discussed random-effects resource selection function, we estimated the effects of sex, age, biological season, mean surface water level, site, and time on selection of each habitat type or spatial feature (i.e. ORV trail, edge) using linear mixed effects models (LMMs). We used AICc to select the most parsimonious model for each habitat type or spatial feature. The LMM results indicate the effect of covariates on selection coefficients. Therefore, LMM covariates could significantly affect selection in the absence of evidence of selection or avoidance.

We also used a two-stage approach to estimate the effects of sex, age, season, surface water depth, site, and time on home range and core area sizes. We quantified monthly home ranges and core areas by taking the 90% and 50% isopleths of the cumulative probability distribution estimated by the random-effects resource selection function. To assess the effects of sex, age, mean water depth, season, study site, and time on home range size, we constructed hypothesis-based candidate LMMs assuming a log normal distribution for each habitat type and spatial feature and used AICc model selection to identify the most parsimonious model.

RESULTS

Estimation of Selection Coefficients and Home Range Size

We estimated monthly resource selection coefficients for diurnal and nocturnal hours as well as 90% home range size and 50% core area size of 141 (*n* = 93 females; *n* = 48 males) white-tailed deer for each month from February 2015 through January 2017 (Tables 3.2, 3.3). At the population level, deer did not select for or against any habitat variable, however we observed a high degree of individual variation in selection of every habitat variable (Table 3.4). The sexes rarely differed in selection, with the exception of marsh habitats. For example, Figure 3.1

illustrates the considerable individual variability in selection of cypress habitat variables during February 2015. Although sex did not affect habitat selection at the population level, we observed sex-specific differences in home range and core area size. We averaged across 12 month periods (February through January) to obtain mean annual home range sizes, which were larger for males (411 ha, 95% CI: 48.6-1821) than females (103 ha, 95% CI: 28.8-271). Similarly, mean annual core area sizes for males (85.2 ha, 95% CI: 9.68-378) were larger than those of females (20.5 ha, 95% CI: 5.40-54.4).

Second-Stage Analysis of Selection Coefficients

For our second stage analysis of the individual-level selection coefficients, we found no evidence that selection varied with age. Similarly, LMM results indicated that sex and biological season only affected selection of marshes. Although we observed no effects of sex or biological season on selection of cypress, ORV trails, prairies, edges, flatwoods, or hammock, we organize the results from those models by sex and season for consideration in the context of the reproductive-strategy hypothesis.

Surface water levels affected selection of every habitat variable with the exception of prairie, which may be explained by a record-setting high water event that occurred in late January 2016 when mean surface water levels peaked at 0.75 m as a result of several intense precipitation events occurring in rapid succession. We observed main effects of water depth on selection of cypress, edge, flatwoods, and hammocks, interactive effects of water depth on selection of marshes, and no effect of water depth on selection of prairies (Table 3.5). The most supported models for selection of edge and hammock included only the main effect of water depth. Females selected against edge during the rearing season of 2015 and the gestation season of 2016, both periods of relatively low or decreasing water levels, and only selected for edges during the late rearing 2015 and late gestation 2015, periods of relatively high water (Figs. 3.2, 3.3). While we observed no selection for hammocks, we found a positive effect of water depth on selection of hammocks (Fig. 3.4). Selection for cypress increased with water depth, although the effect was stronger in 2015 than during the high water events of 2016 (Fig. 3.5). We observed a positive correlation between selection of flatwoods and mean water depth (Fig. 3.6). Male selection for flatwoods occurred during the dry fawning and rearing seasons of 2015. Males only selected against flatwoods during the rut, post-rut, and gestation season of 2016. Females showed no selection of flatwoods except during both fawning seasons, rearing of 2015, and post-rut of 2016 when they selected for flatwoods habitats. Both male and female selection of marshes decreased with increasing water depth, however males more strongly avoided marshes during high water (Fig. 3.7). Water depth also interacted with study site, which we included to assess the effects of the hydrological gradient across sites, such that deer on FPNWR exhibited avoidance of marshes during March and April 2015, a relatively dry period, while deer on BI and AL selected for marsh during these times. Similarly, on FPNWR, we observed no selection for or against marshes during high water events in early 2016 when deer on BI and AL avoided marshes (Fig. 3.8).

We observed main effects of diel time period on selection of cypress, ORV trails, and flatwoods as well as an interactive effect of time and season on selection of marshes, which we included to test the hypothesis that biological season would influence selection of habitat in the context of the “risky times hypothesis”. Females selected for cypress during nocturnal hours of the 2015 rut and post-rut seasons while males selected for cypress during nocturnal hours of September 2015 (early post-rut). The most supported model for selection of ORV trails included only the main effect of time. Both sexes exhibited increased selection for ORV trails during gestation and rut seasons, but selection of ORV trails decreased during nocturnal hours (Fig. 3.9). The interactive effect of time and season on selection of marshes is evidenced by female selection for marshes during high-risk, nocturnal hours of both fawn-rearing seasons and avoidance of marshes during nocturnal hours of the 2015 gestation and 2016 fawning seasons, periods of high water. Time affected selection of flatwoods such that nocturnal selection by males increased during the flooded fawning, rearing, and pre-rut seasons of 2016. Nocturnal selection of flatwoods also increased during both gestation seasons (Fig. 3.10). When there was a difference in day and night selection of flatwoods by females, they generally selected for flatwoods during the diurnal hours, except during gestation seasons of both years, when they selected for flatwoods at night but exhibited no selection during the day. We observed no effect of time on selection of forest edges, however females selected against edge during nocturnal hours during both rearing seasons and only selected for edge at night during pre-rut 2015 and late rearing 2016, both periods of rapidly rising water levels. Females selected for edge during diurnal hours only during periods of high water and against edges during diurnal hours of gestation 2016. Males selected for edge during day and night of the dry, 2015 rut and during the wet post-rut of 2016. The most dramatic difference in diel selection of edge by males was during April 2015 (rearing season) when males selected for edge during diurnal hours and against edge during nocturnal hours as surface water levels were decreasing.

Second-stage analysis of home range and core area size

There were 4 supported models for home range size, and they included sex, season, mean water depth, and site as predictor variables (Table 3.6). We observed effects of mean water depth and study site on home range size of deer as well as an interactive effect of sex and season. Home range size increased with increasing water depth for both sexes. For example, mean female home range sizes differed substantially between March of 2015 (93.1 ± 4.46 ha; mean ± SE), a dry year, and March 2016 (135 ± 16.3), a period of relatively high surface water levels (Figs. 3.11, 3.12). Males similarly increased home range size with increased water depth as indicated by an increase from June 2015 (445 ± 115 ha) to June 2016 (842 ± 236 ha) (Fig. 3.13). Deer home ranges on FPNWR were smaller than those on BI and AL, which did not differ. Seasonally, the sexes differed with respect to trends in home range size over time. Male home ranges were smallest during the gestation and fawning seasons and generally increased through time, peaked during the pre-rut and rut, and decreased dramatically during the post-rut. Conversely, female home ranges generally decreased throughout the fawning season, were smallest during the rearing season, and increased as the rut approached however the largest mean female home range size (487 ± 130 ha) occurred during the 2016 fawning season, a period of record-setting mean water depth.

Model selection supported two models estimating the effects of sex, season, mean water depth, and site on core area size, which we averaged for inference. We observed interactive depth *x* site and sex *x* season effects on core area size. Male core area size followed similar patterns in size as home range size for both sexes; however the variation in core area size was greater for males (Figs. 3.14, 3.15). The interaction between mean water depth and site is evidenced by smaller core area sizes in FPNWR relative to BI and AL during high water events occurring during the post-rut of 2015 and fawning and rut seasons of 2016. Notably, we documented the smallest (9.36 ha ± 0.72; mean ± SE) and largest mean male core area size on AL (462 ha ± 164) during the dry 2015 rearing and wet 2016 fawning seasons, respectively.

DISCUSSION

Our results indicate that space use of deer in the BCB is linked to seasonal variation in the hydrological regime. We documented limited sex-specific variation in habitat selection, however sex strongly predicted home range size and core area. We hypothesize that extremely high water levels during our study limited resource availability and forced the sexes to utilize similar resources. Our results also indicate that biological season influences space use, as home range and resource selection patterns differed between the sexes according to the reproductive cycle. Additionally, diel variability in selection of landscape features such as forest edge and ORV trails suggests that deer perceive these areas as high-risk spaces to be avoided at high-risk times (night), which supports the 'risky places' and 'risky times' hypothesis of predator avoidance.

We documented strong effects of seasonal hydrological shifts on habitat selection and home range size deer in the BCB. Unlike Sargent (1992) and Miller (1993), we observed effects of water depth on selection of every habitat type and spatial feature except for prairies, perhaps because their Everglades study occurred during relatively dry years. However, our findings agree with those of MacDonald-Beyers and Labisky (2005) who documented strong effects of flooding on deer populations in the Everglades. Specifically, they reported significant increases in selection of hardwood hammock islands during a high-water event. While our results indicate significant shifts in selection of hammock that were positively correlated with mean water depth, we observed no selection for or avoidance of hammock, perhaps due to greater availability of pine flatwoods on our study sites. Pine flatwoods typically remain dry throughout the year, and our results indicate that they are used disproportionately to availability during periods of high water levels by both males and females.

Surface water levels affected selection of marshes, which typically experience the greatest water depths. Both sexes exhibited selection for marshes during dry periods and elevated water levels resulted in no selection of these habitats by males while inducing avoidance by females. Extremely atypical flooding during what is generally a relatively dry period may explain female avoidance during this period. MacDonald and Labisky (2005) reported negative impacts of flooding on fawn survival suggesting that, where possible, females should seek the driest possible habitat leading up to parturition. Female selection of marshes during the rearing period of both years may indicate relatively high habitat quality considering the energetic costs of lactation. However, we caveat our observed effects of hydrology on space use by acknowledging our study encompassed only 2 years within a system characterized by high annual variation in rainfall. Continued remote-monitoring of deer habitat selection over a broader timescale will be necessary to validate our results.

Sexual segregation in ungulates is influenced by species-specific life history, predator communities, social structure, and environmental factors (Barboza and Bowyer 2000, Ruckstuhl and Neuhaus 2002, Main et al. 1996). The reproductive-strategy hypothesis states that energetic demands associated with reproduction drive divergence in the behavior of the sexes, thus inducing spatial segregation outside of the breeding season (Main et al. 1996). In our study, the sexes differed most in selection during the fawning and rearing season, thus providing evidence of support for the reproductive-strategy hypothesis. Selection generally differed less during the wet 2016 fawning and rearing seasons relative to the dry 2015 fawning and rearing seasons suggesting limited resources may reduce spatial segregation of the sexes in the BCB. The observation that both male and female home ranges increased during of periods of high water, while female core area size changed little relative to that of males, provides additional evidence for the reproductive-strategy hypothesis. This supports the prediction that males should seek abundant forages while females occupy areas with dependable resources. While inundation may increase overall area of use by females, they maintain fidelity to similarly sized core areas regardless of surface water levels.

To assess the effects of risk of predation by panthers on resource selection, we examined selection of ORV trails, known to be high-use travel corridors for panthers (Crawford, D. A., *unpublished data*), and forest edges, which afford concealment cover to predators, as risky places where nocturnal hours are relatively high-risk times. Our results support the 'risky-times' and 'risky-places' hypotheses as evidenced by the aversion of the sexes to potentially high-risk areas, particularly during relatively high-risk times. For example, deer generally showed no selection for ORV trails except during peaks in surface water depths and reserved activity near trails for low-risk diurnal hours. In addition, deer avoided edges during relatively dry periods, specifically during high-risk nocturnal hours, and selection for edges only occurred during periods of peak surface water depths when open habitat types were flooded. Under the reproductive-strategy hypothesis framework, females perceived edges to be particularly risky at night as evidenced by either no selection or selection for edges during diurnal hours versus avoidance of edges at night during the fawning and rearing seasons.

As resource availability decreases and exposure to risk of predation increases due to necessitated use of otherwise avoided areas, individuals must renegotiate energy budgets as they attempt to forage optimally. Furthermore, strong positive correlation between forest edge selection and mean water depth during the fawning and rearing seasons supports this mode of logic, as females should select for the safest habitats when offspring are most vulnerable to predation. Our results offer evidence of an interaction between hydrology and risk of predation, however experimental quantification of perceived risk of predation relative to habitat types and spatial features is required to isolate risk as the causal mechanism of habitat avoidance. We recommend the use of giving-up densities experiments (e.g., Altendorf et al. 2001, Rieucau et al. 2009) in future research for estimation of relative perceived risk.

MANAGEMENT IMPLICATIONS

Increased utilization of relatively dry habitats such as pine flatwoods and hardwood hammocks suggests that these habitats provide refugia for deer from flood waters during periods of inundation. Therefore, management actions intended to improve habitat quality and availability of forage should focus on these habitats in an effort to offset limited forage availability experienced as result of widespread inundation. Additionally, the use of closed canopy habitats during periods of relatively high surface water levels may affect detection probability of deer during aerial surveys, the primary census method employed by managers, which could result in underestimation of population abundance. Managers should attempt to conduct aerial surveys when water levels are lowest to most effectively mitigate reduced detection probability. Management strategies focused on maintaining sustainable deer herds in the region as a human resource and prey base for the Florida panther should consider the potential adverse effects of extreme hydrological fluctuations on regional deer populations (i.e. increased depredation, decreased forage availability) in terms of issuing harvest permits and setting harvest goals.

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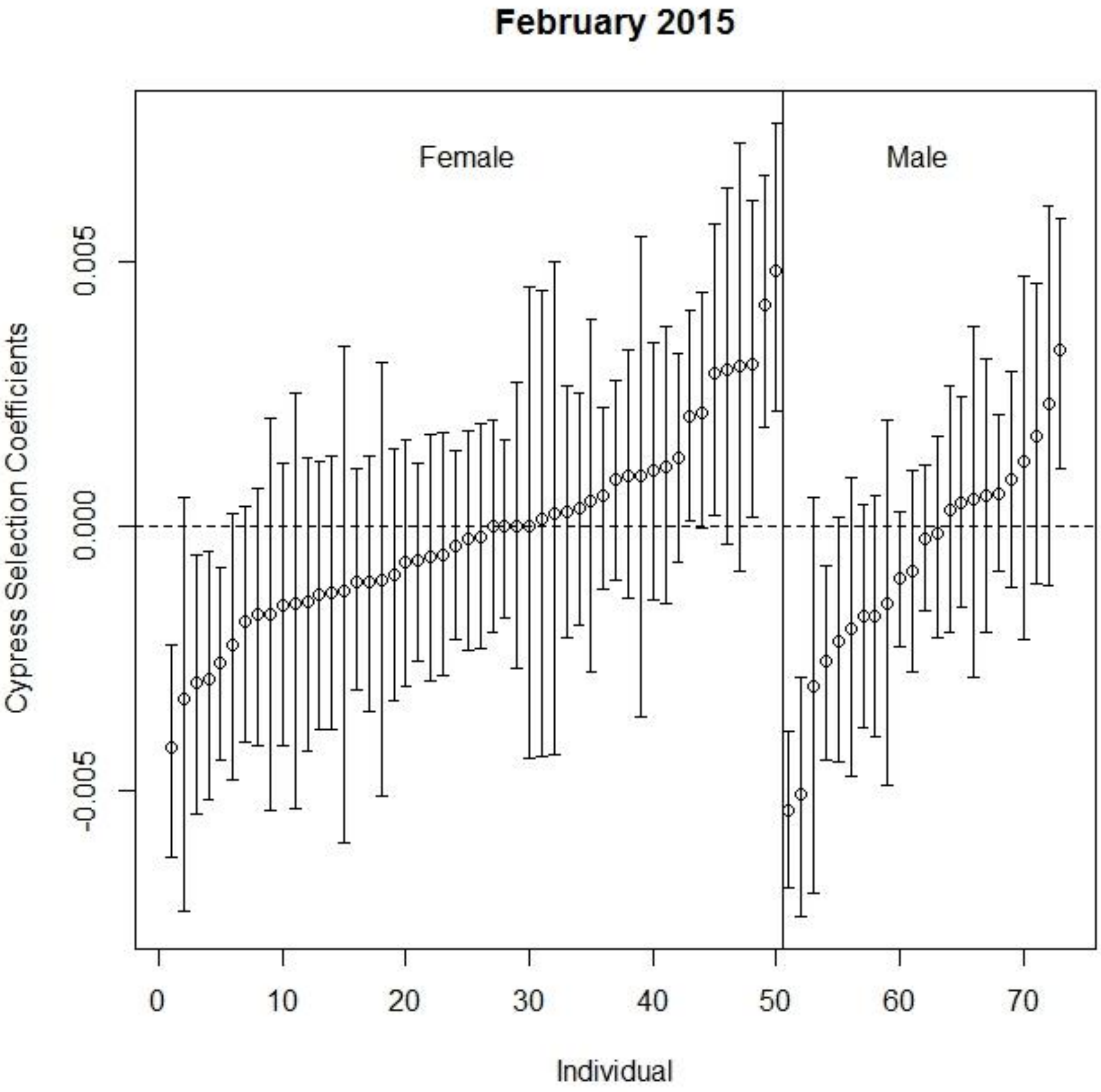

Fig. 3.1. Cypress selection coefficients estimated for male and female deer for February 2015 using a distance-based Poisson point process model, Big Cypress Basin, Florida. Error bars represent 95% credible intervals calculated using 5000 Markov chain Monte Carlo (MCMC) samples from the posterior distribution.

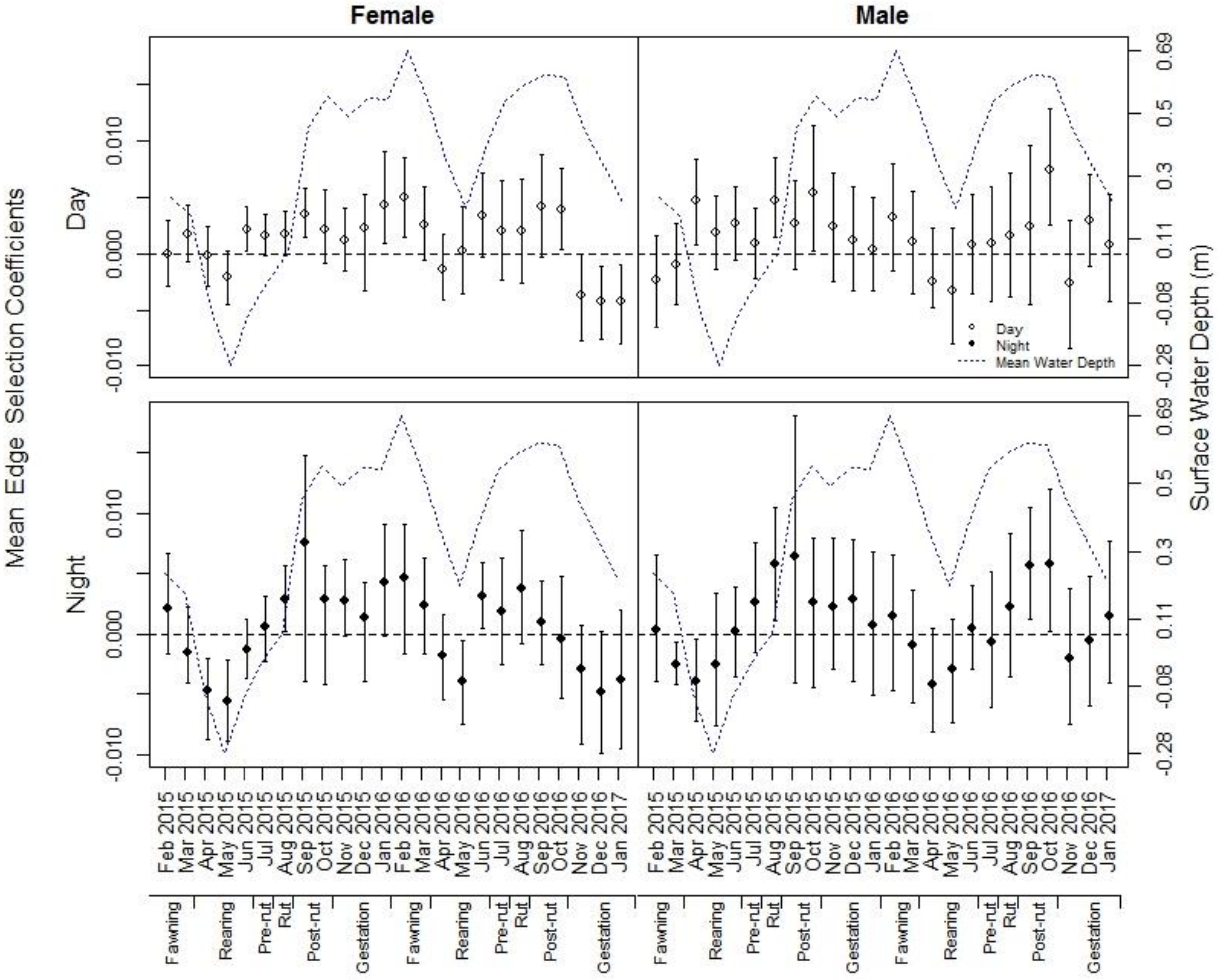

Figure 3.2. Mean sex-specific selection coefficients for forest edges during diurnal (hollow dots) and nocturnal hours (solid dots) across all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for edge, and upper CIs less than zero indicate avoidance of edges.

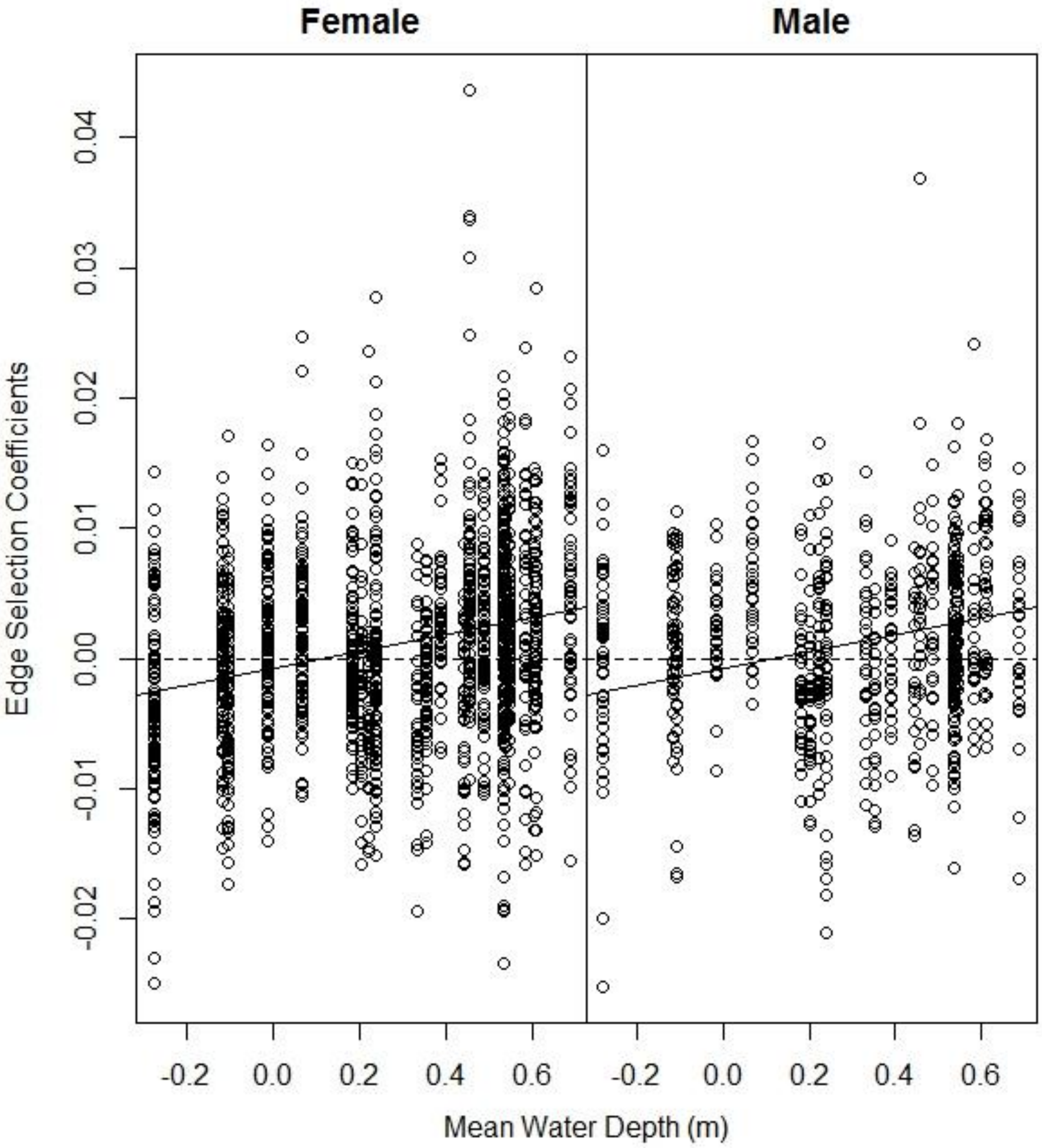

Figure 3.3. Scatterplot of individual deer forest edge selection coefficients over mean water depth in meters, Big Cypress Basin, Florida. The solid line indicates the regression line for the estimated effect of water depth on selection of edge from second-stage linear mixed model output.

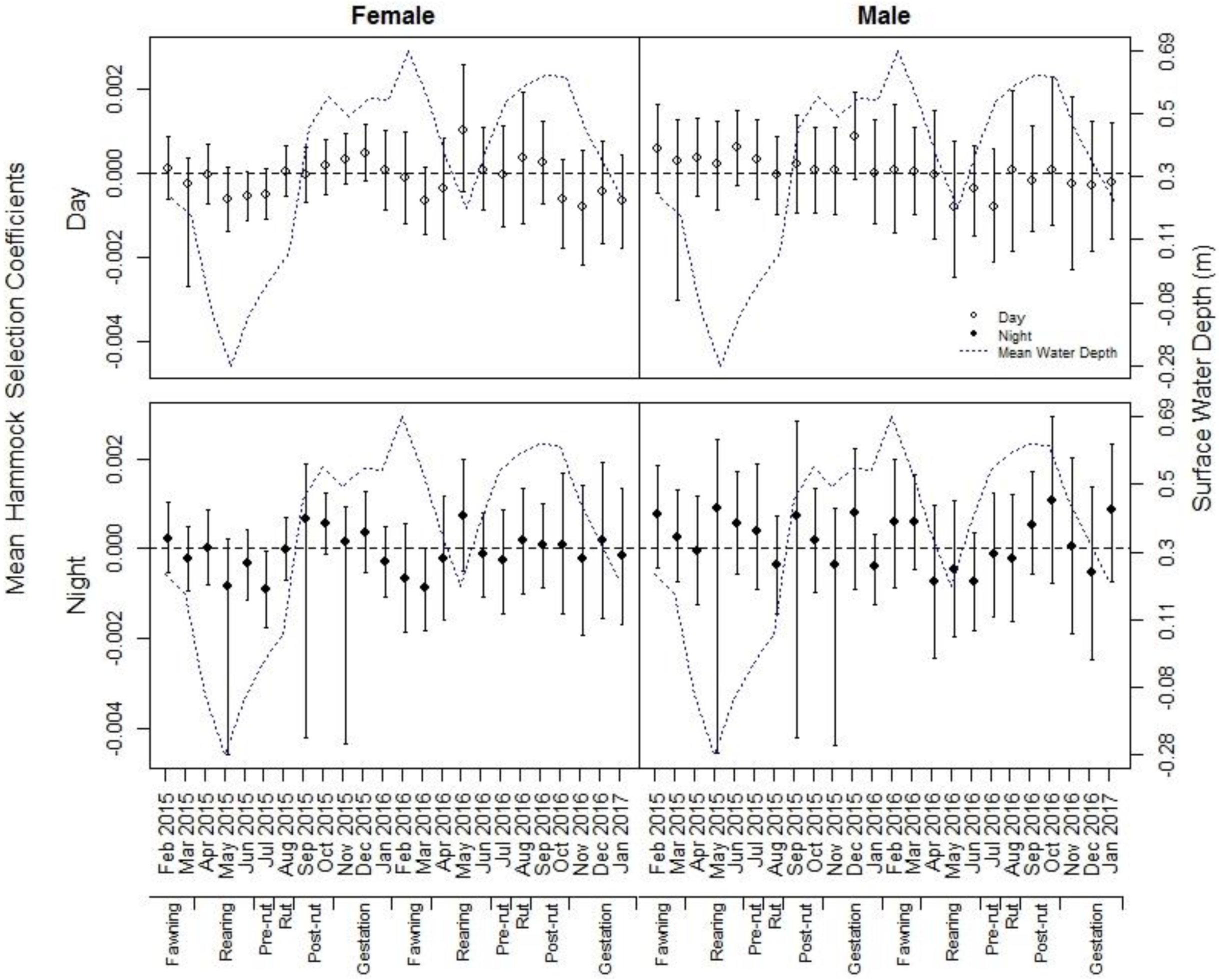

Figure 3.4. Mean sex-specific selection coefficients for hammocks during diurnal (hollow dots) and nocturnal hours (solid dots) across all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for hammocks, and upper CIs less than zero indicate avoidance of hammocks.

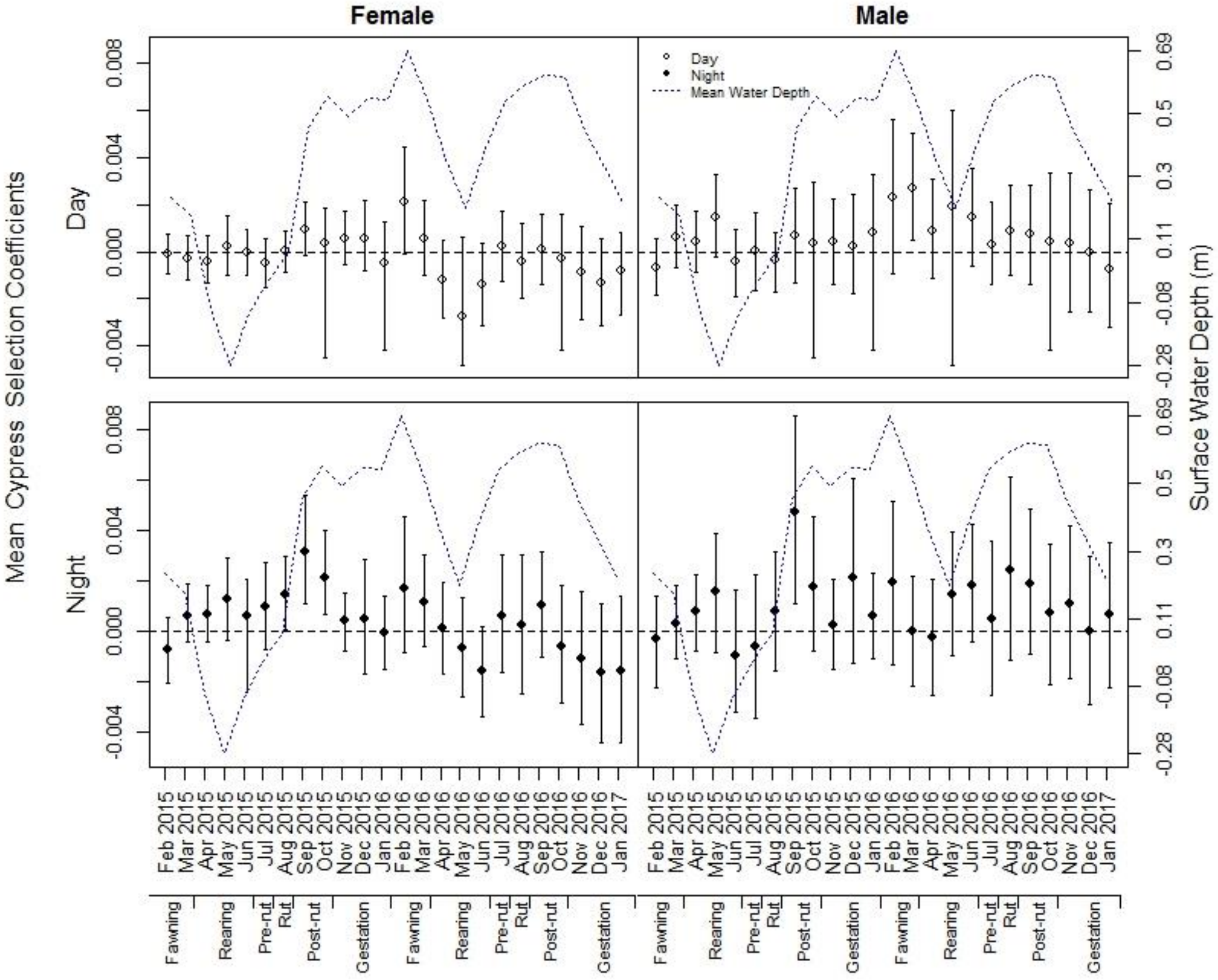

Figure 3.5. Mean sex-specific selection coefficients for cypress communities during diurnal (hollow dots) and nocturnal hours (solid dots) across all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for cypress, and upper CIs less than zero indicate avoidance of cypress.

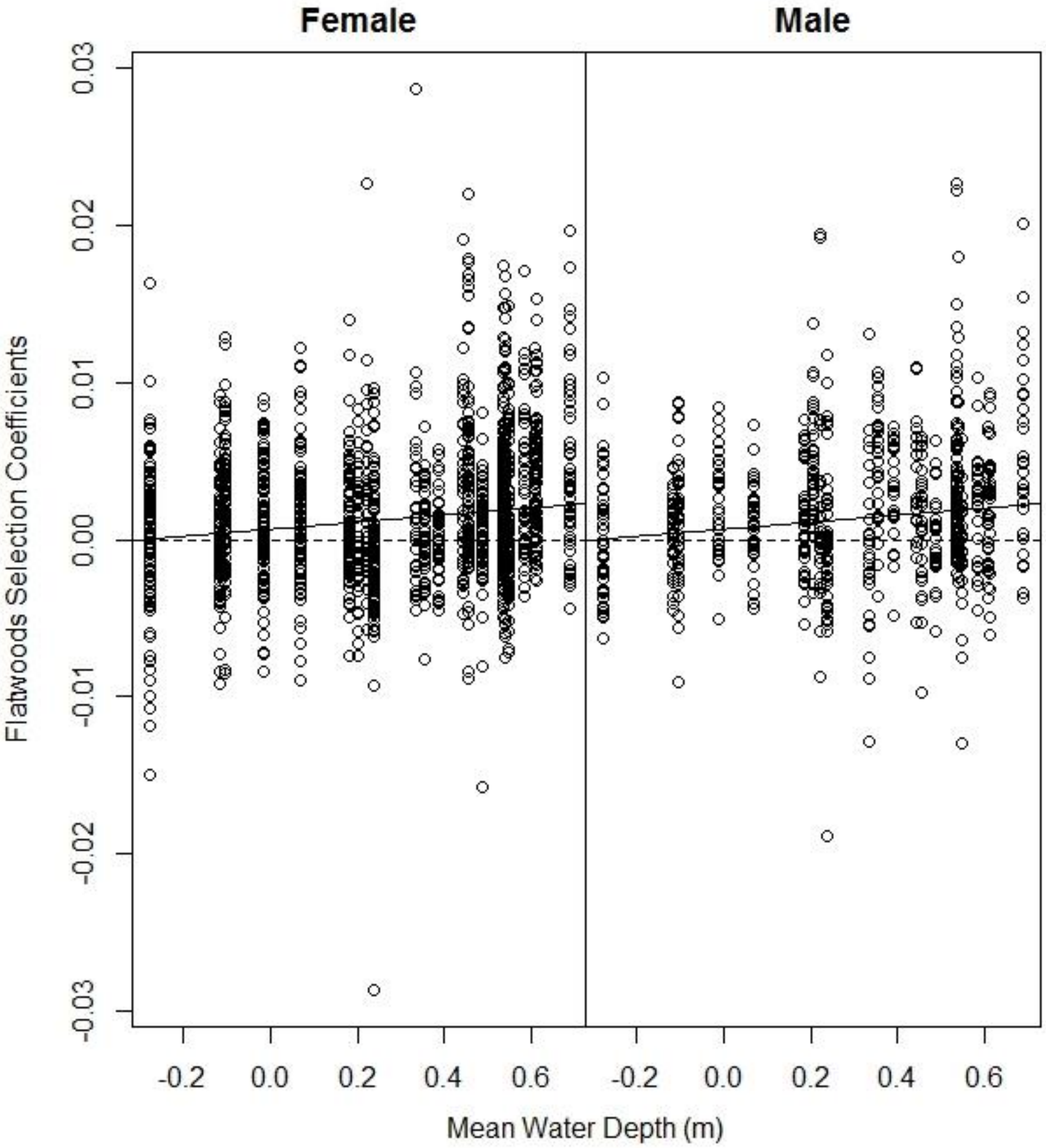

Figure 3.6. Scatterplot of individual flatwoods selection coefficients over mean water depth in meters, Big Cypress Basin, Florida. The solid line indicates the regression line for the estimated effect of water depth on selection of flatwoods from second-stage linear mixed model output.

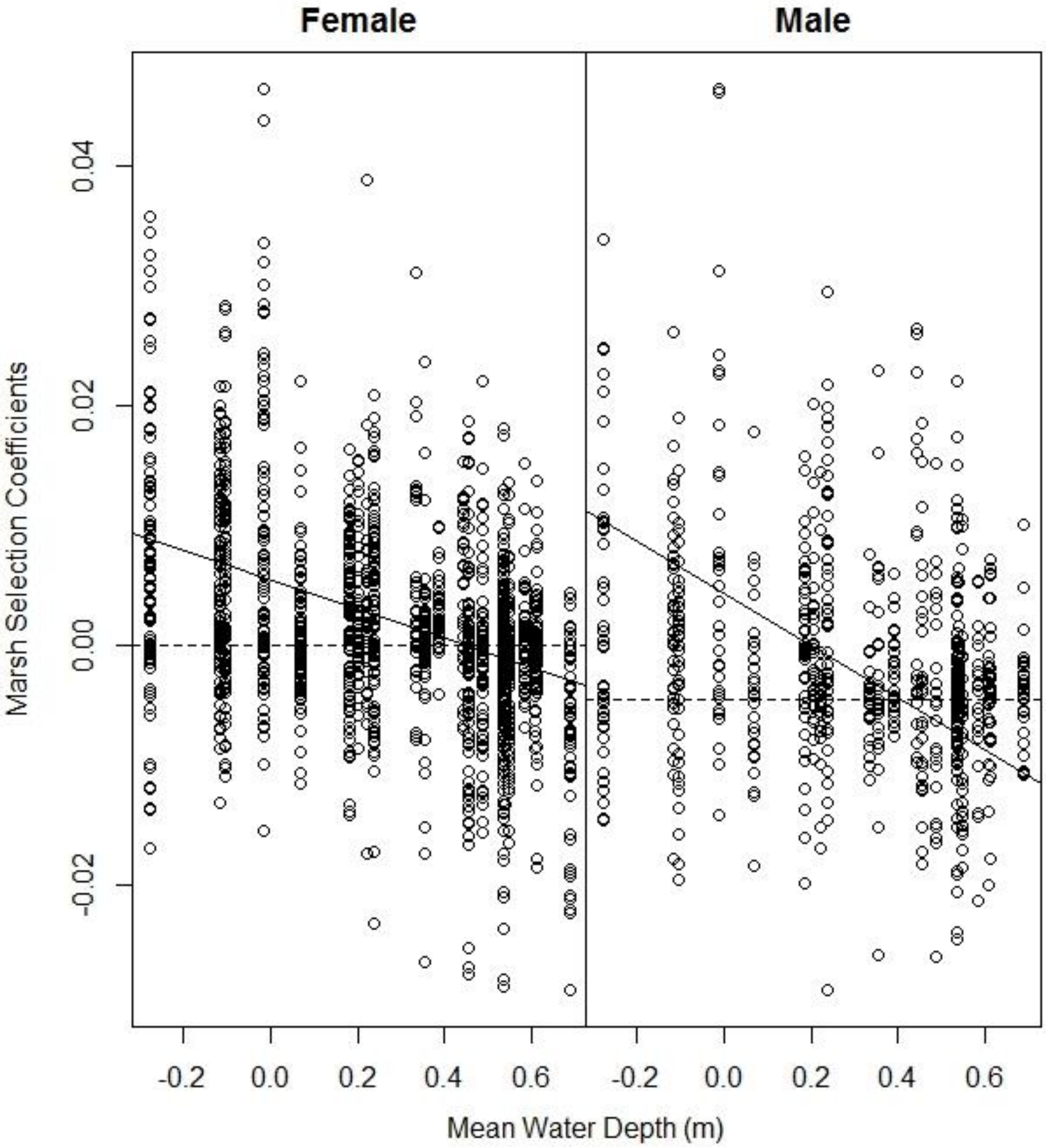

Figure 3.7. Scatterplot of individual marsh selection coefficients over mean water depth in meters, Big Cypress Basin, Florida. The solid line indicates the regression line for the estimated effect of water depth on selection of of marsh from second-stage linear mixed model output.

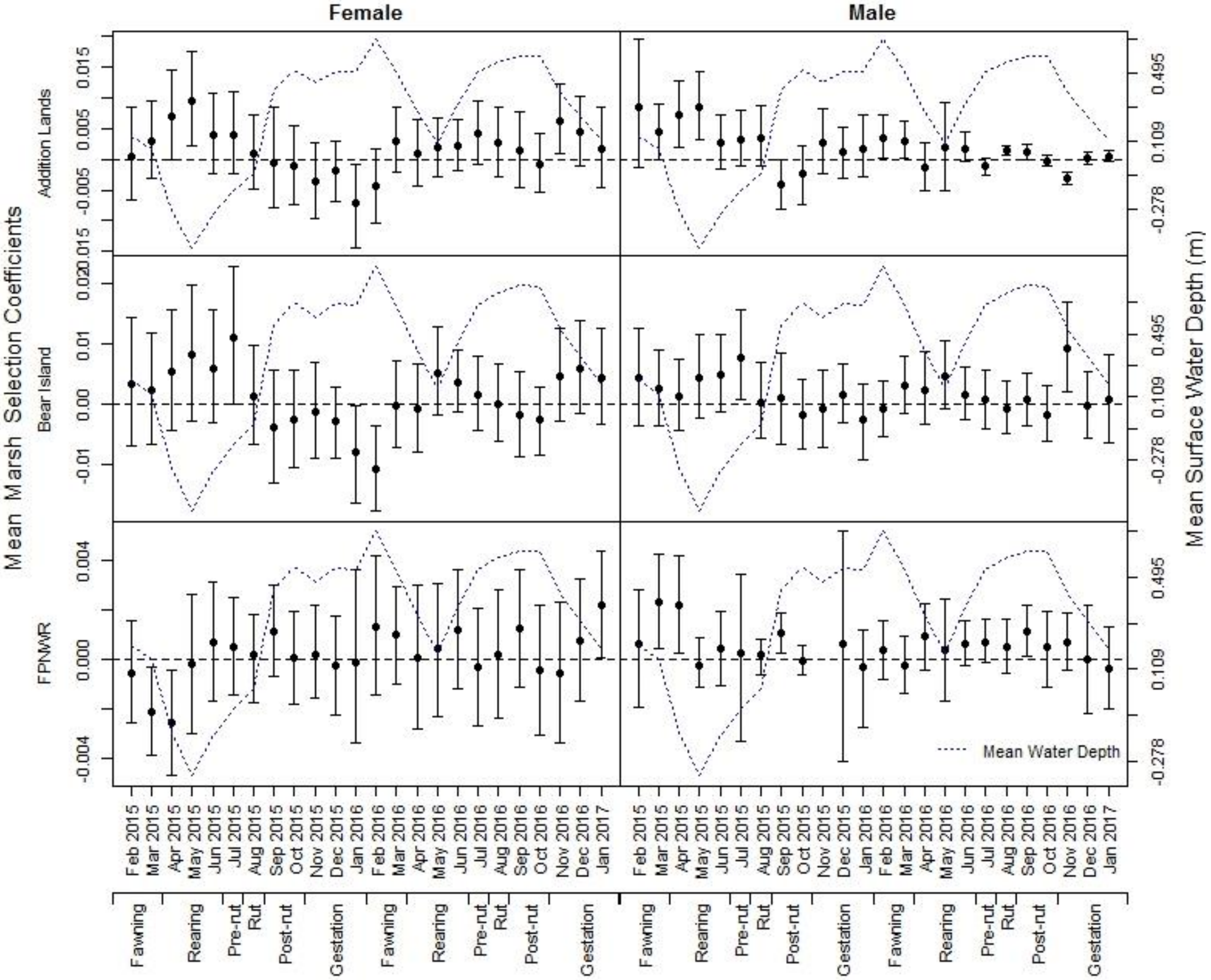

Figure 3.8. Mean sex-specific selection coefficients for marshes on each site, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for marshes, and upper CIs less than zero indicate avoidance of marshes.

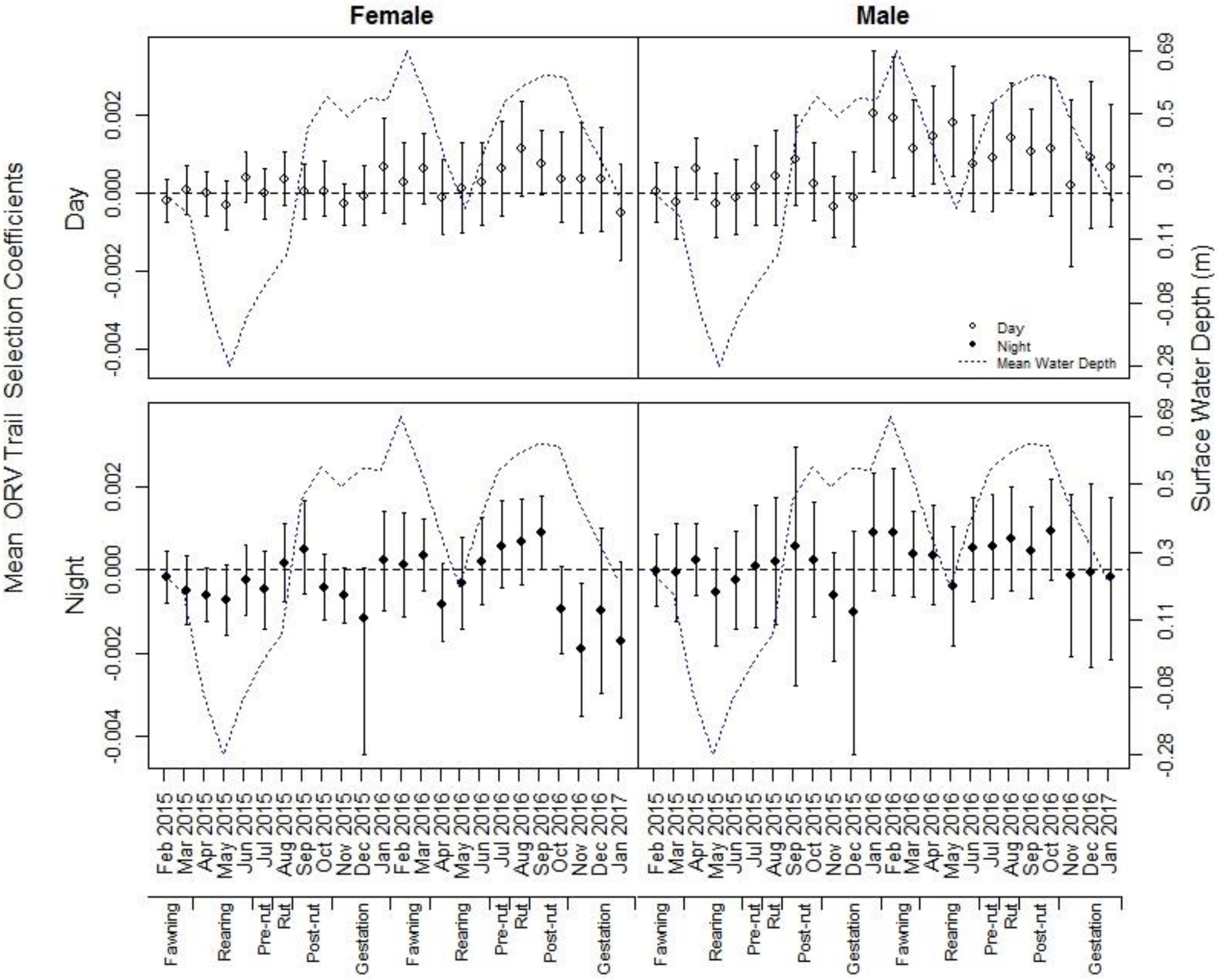

Figure 3.9. Mean sex-specific selection coefficients for ORV trails during diurnal (hollow dots) and nocturnal hours (solid dots) across all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for ORV trails, and upper CIs less than zero indicate avoidance of ORV trails.

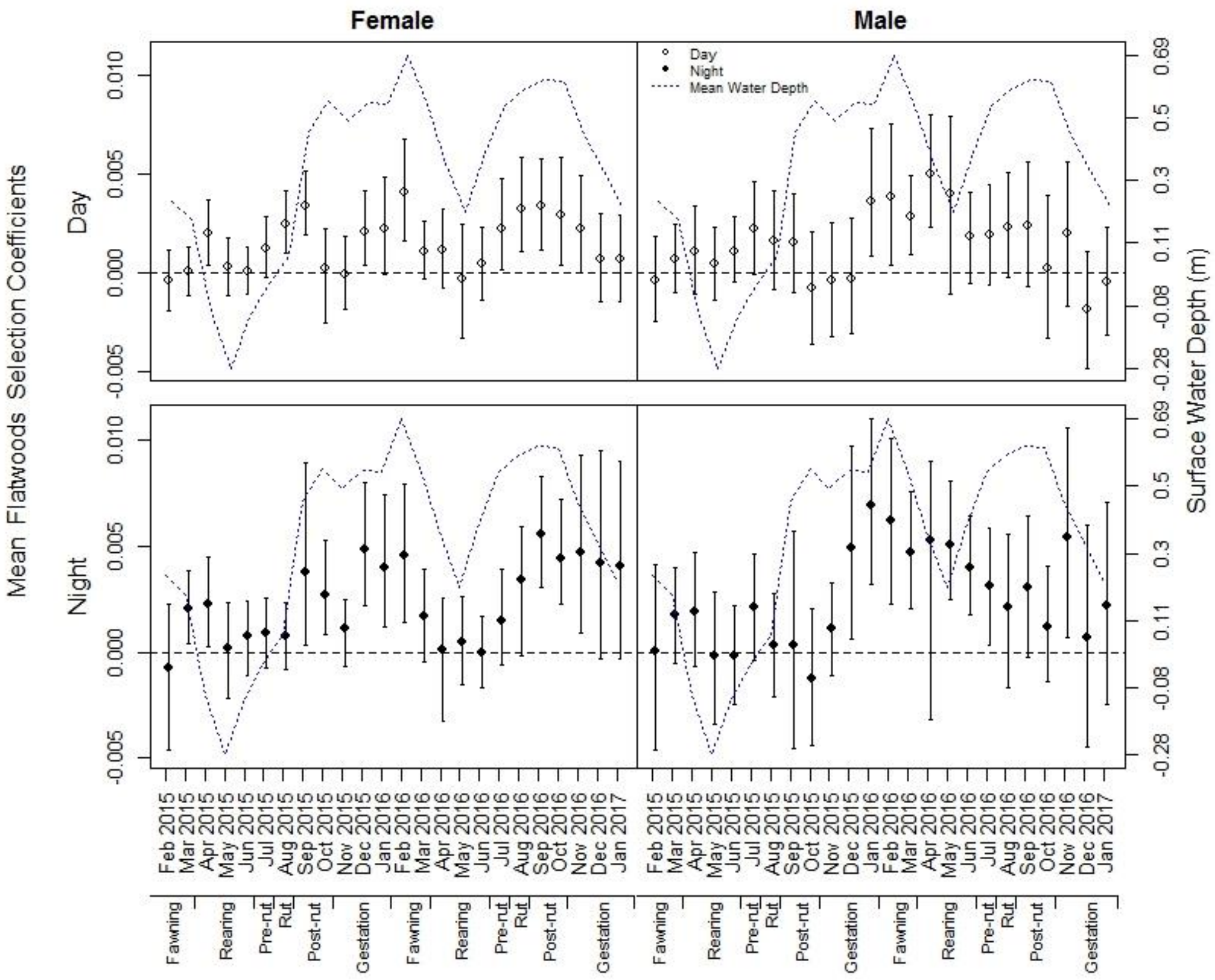

Figure 3.10. Mean sex-specific selection coefficients for pine flatwoods during diurnal (hollow dots) and nocturnal hours (solid dots) across all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. The dashed horizontal line has a y-intercept = 0. CIs overlapping 0 indicate no selection, lower CIs greater than zero indicate selection for flatwoods, and upper CIs less than zero indicate avoidance of flatwoods.

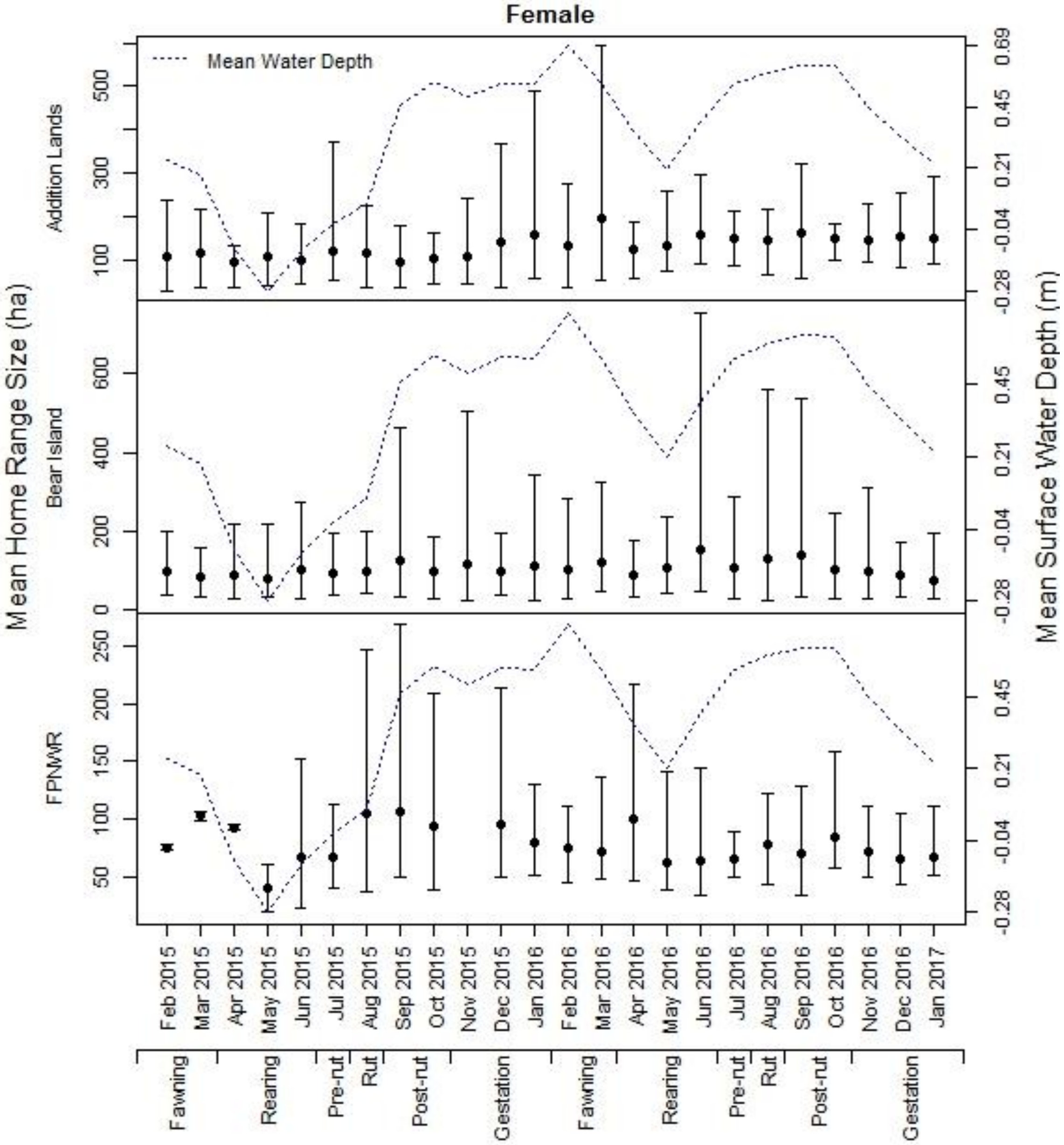

Figure 3.11. Mean female 90% home range sizes on each site for each month of the study. The dotted line indicates mean monthly surface water levels, Big Cypress Basin, Florida. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples.

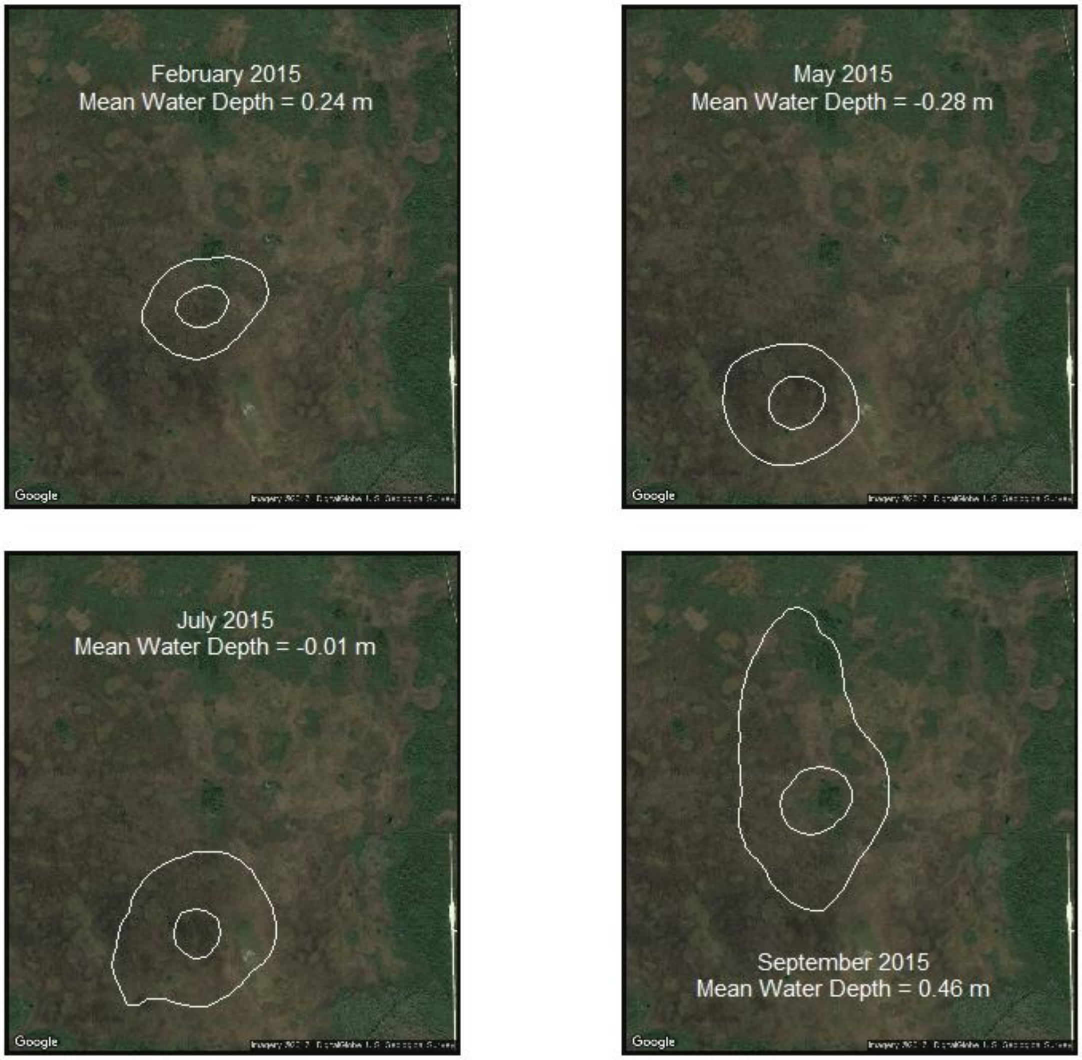

Figure 3.12. Outer contours represent 90% home ranges, and inner contours represent 50% core areas during February, May, July, and September of 2015 for a female residing in an expansive marsh on the Bear Island unit of Big Cypress National Preserve, Big Cypress Basin, Florida. All maps are centered on a small hardwood hammock tree island located in the marsh. Mean water depths for each month are reported in meters.

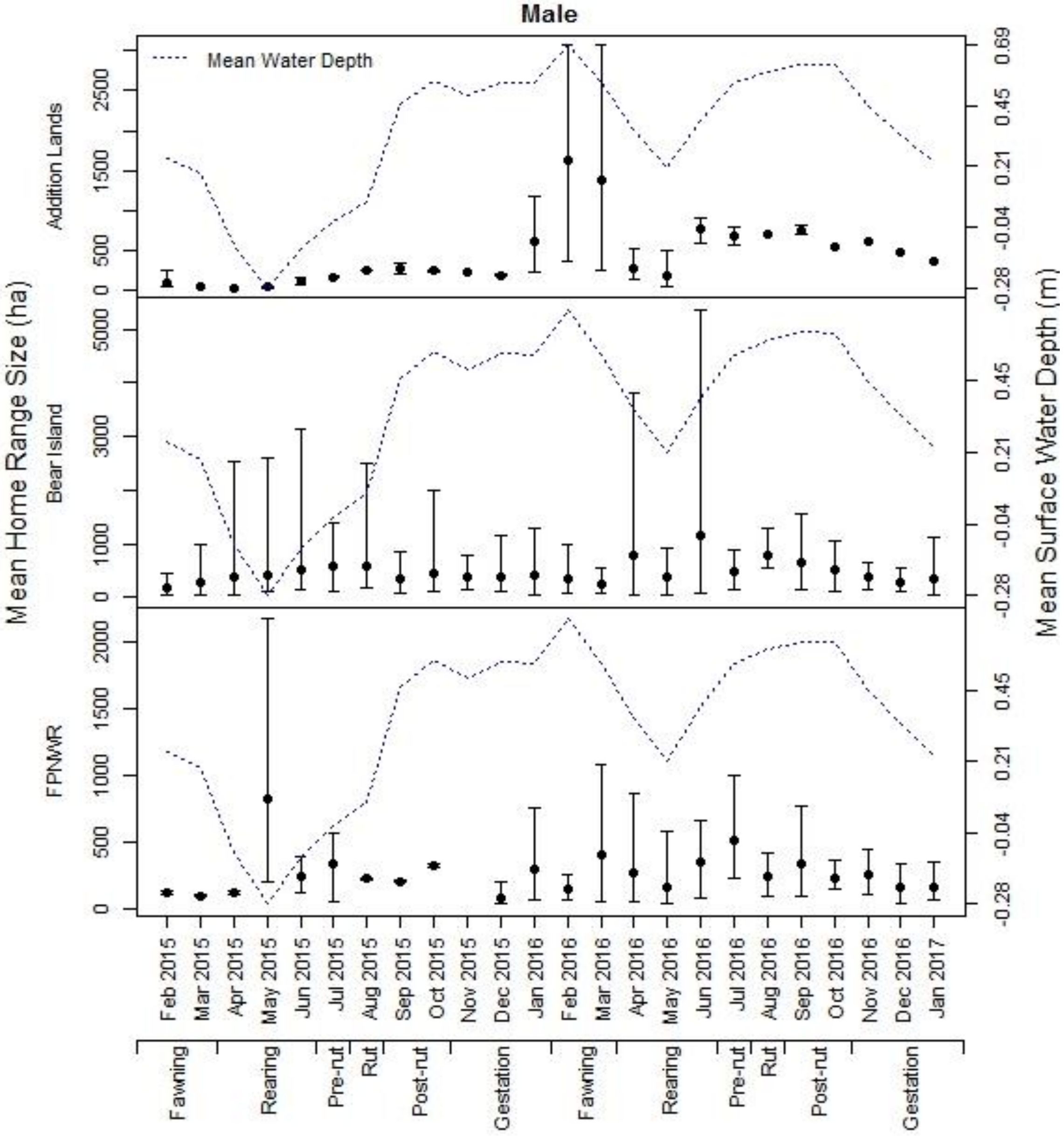

Figure 3.13. Mean male 90% home range sizes on each site through all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples.

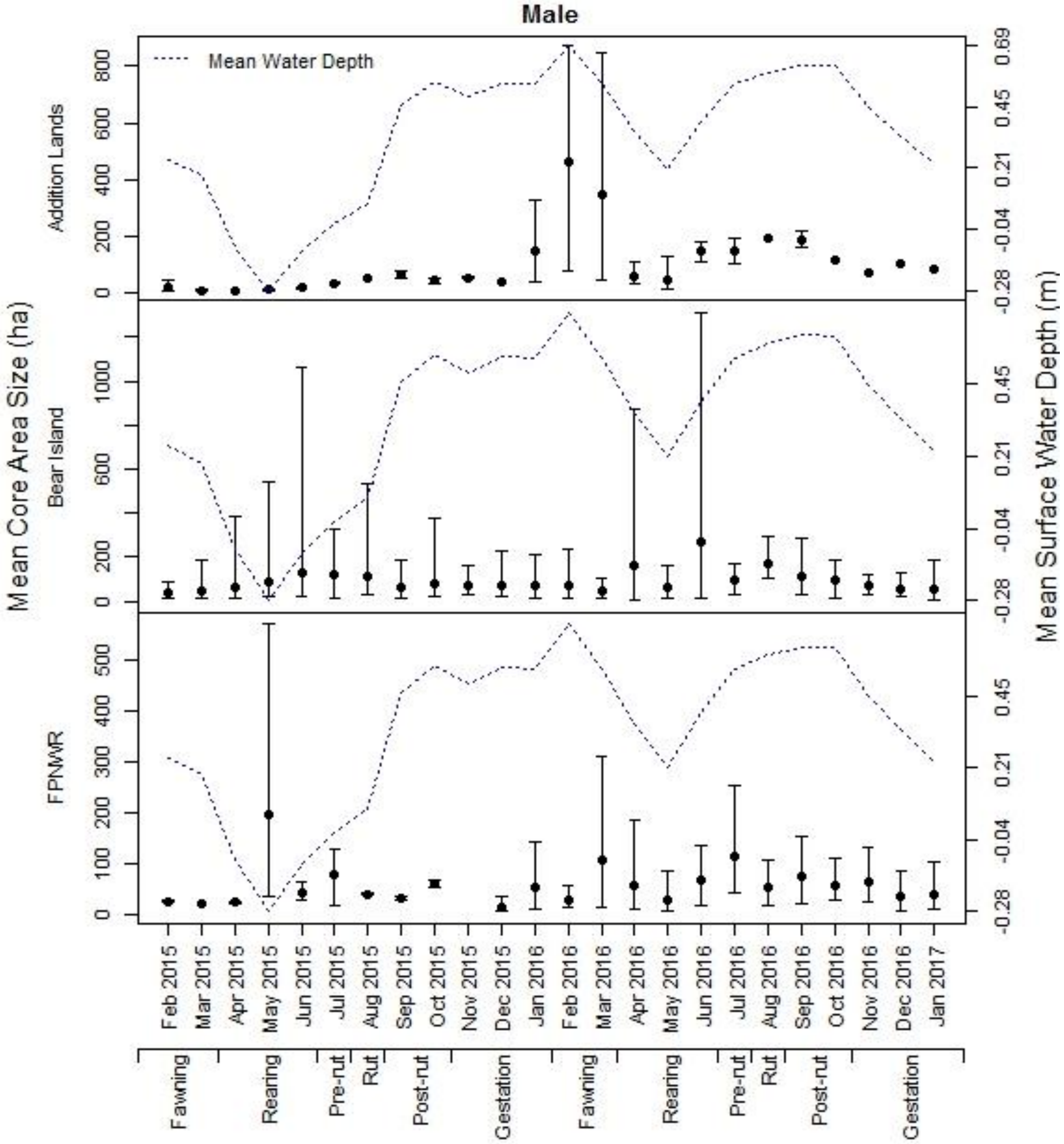

Figure 3.14. Mean male 50% core areas size on each site through all months and biological seasons of the study, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples. Missing values indicate no animals on that site during that period.

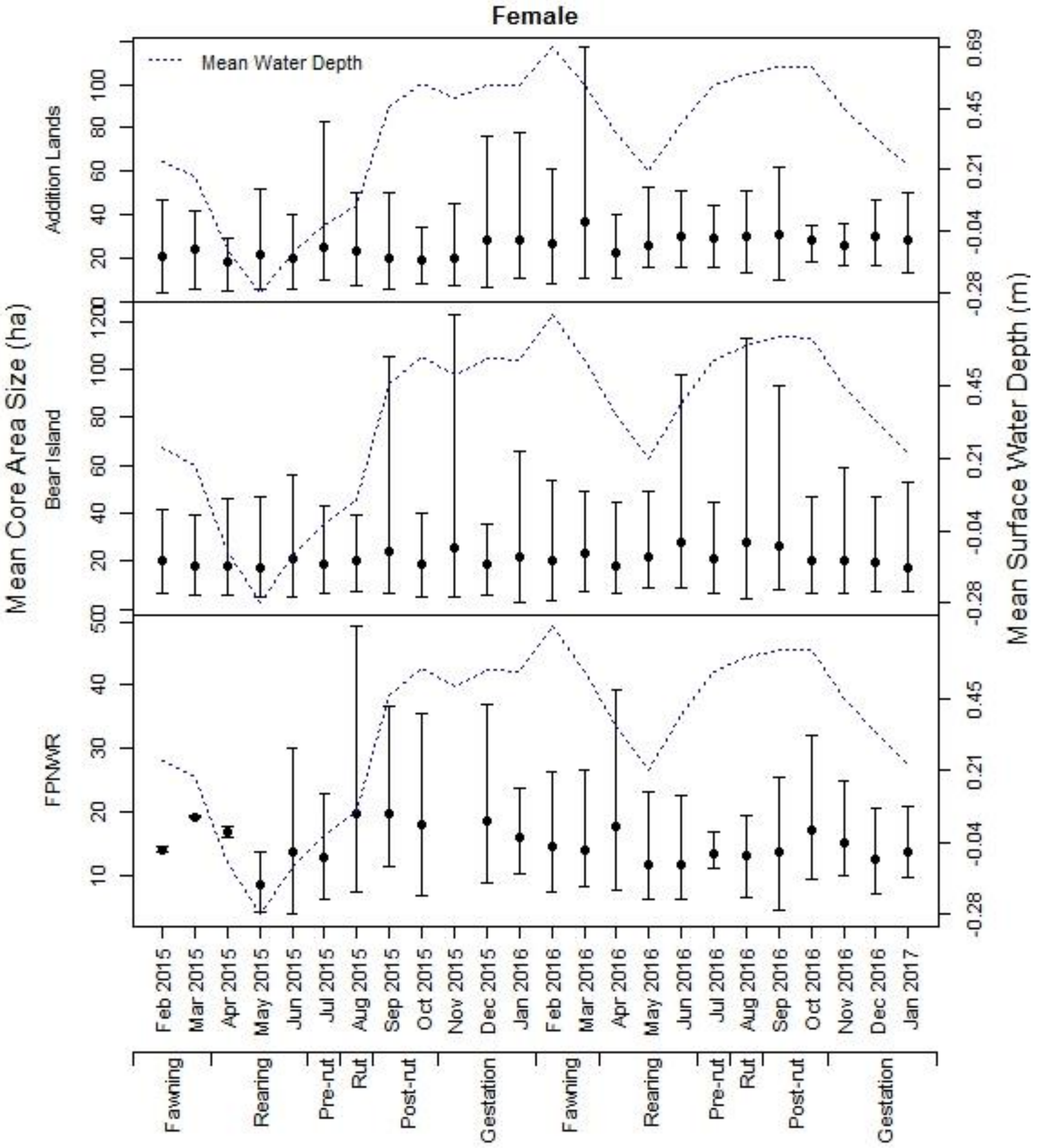

Figure 3.15. Mean female 50% core area sizes on each site through all months and biological seasons, Big Cypress Basin, Florida. The dotted line indicates mean monthly surface water levels. Error bars indicate 95% confidence intervals (CIs) calculated from monthly samples.

Table 3.1. The number of individual selection coefficients and home ranges estimated during each month of the study is presented by site and sex, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

	Bear Island		Addition Lands		FPNWR		
Month	Male	Female	Male	Female	Male	Female	Total
Feb-15	20	36	3	13	1	1	74
Mar-15	19	33	1	12	1	1	67
Apr-15	18	32	1	11	1	1	64
May-15	18	31	1	11	3	7	71
Jun-15	15	29	1	10	2	10	67
Jul-15	15	29	1	10	2	10	67
Aug-15	13	27	1	10	1	9	61
Sep-15	11	26	1	10	1	9	58
Oct-15	11	25	1	10	1	9	57
Nov-15	11	22	1	9	0	8	51
Dec-15	10	20	1	9	4	8	52
Jan-16	11	23	3	8	5	4	54
Feb-16	8	19	3	7	5	4	46
Mar-16	8	17	3	7	5	4	44
Apr-16	8	15	2	6	5	5	41
May-16	8	14	3	6	6	5	42
Jun-16	8	14	2	6	5	5	40
Jul-16	8	14	2	6	5	5	40
Aug-16	8	14	1	6	5	5	39
Sep-16	7	13	1	6	5	5	37
Oct-16	6	12	1	6	5	5	35
Nov-16	6	11	1	6	4	5	33
Dec-16	4	11	1	6	9	5	36
Jan-17	6	11	1	6	10	5	39

Table 3.2. Age, site, number of diurnal locations (N_d), number of nocturnal locations (N_n), and number of total locations for male white-tailed deer included in analyses of habitat selection, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

ID	**Sex**	**Age**	**Site**	**N_d**	**N_n**	**Total**	**ID**	**Sex**	**Age**	**Site**	**N_d**	**N_n**	**Total**
103	m	3	FP	395	425	820	222	m	3	FP	490	480	970
109	m	2	BI	235	254	489	231	m	4	FP	1193	1288	2481
113	m	4	AL	160	178	338	232	m	2	FP	877	874	1751
114	m	1	BI	689	618	1307	233	m	1	FP	502	531	1033
121	m	3	BI	276	272	548	235	m	2	BI	1124	1232	2356
125	m	2	AL	871	874	1745	247	m	1	FP	1166	1257	2423
128	m	2	BI	762	694	1456	250	m	2	BI	806	785	1591
130	m	2	BI	996	989	1985	254	m	2	BI	1169	1253	2422
137	m	2	BI	159	185	344	255	m	1	BI	1083	1137	2220
141	m	5	BI	985	998	1983	257	m	5	AL	659	634	1293
143	m	1	BI	476	434	910	258	m	1	BI	1166	1254	2420
148	m	2	BI	1010	1013	2023	260	m	2	FP	1191	1287	2478
149	m	2	BI	987	1004	1991	266	m	2	BI	1170	1255	2425
157	m	1	BI	401	400	801	283	m	1	AL	297	341	638
161	m	3	BI	614	565	1179	289	m	3	BI	751	702	1453
176	m	3	BI	414	407	821	294	m	3	BI	1076	1025	2101
179	m	2	BI	1011	1034	2045	313	m	4	AL	957	978	1935
186	m	2	BI	988	1021	2009	316	m	1	BI	91	116	207
191	m	3	BI	977	1023	2000	322	m	2	FP	759	817	1576
197	m	3	BI	976	988	1964	400	m	2	FP	117	161	278
198	m	4	BI	760	708	1468	401	m	3	FP	114	175	289
204	m	3	BI	980	1002	1982	405	m	3	FP	93	127	220
205	m	3	BI	955	939	1894	406	m	4	FP	104	152	256
219	m	3	FP	120	97	217	407	m	2	FP	108	156	264

Table 3.3. Listed are the age, site, number of diurnal locations (N_d), number of nocturnal locations (N_n), and number of total locations for each female included in analyses, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

ID	**Sex**	**Age**	**Site**	**N_d**	**N_n**	**Total**	**ID**	**Sex**	**Age**	**Site**	**N_d**	**N_n**	**Total**
106	f	2	BI	1011	1033	2044	202	f	2	AL	165	187	352
107	f	3	BI	1008	1020	2028	203	f	1	BI	849	807	1656
110	f	2	BI	816	782	1598	206	f	3	BI	948	919	1867
112	f	2	BI	991	949	1940	214	f	2	FP	691	698	1389
115	f	2	BI	439	427	866	216	f	3	FP	432	341	773
117	f	3	FP	916	968	1884	220	f	2	FP	591	569	1160
118	f	2	BI	1003	1014	2017	221	f	2	FP	213	167	380
119	f	4	BI	994	1005	1999	223	f	3	FP	673	680	1353
120	f	3	BI	711	658	1369	224	f	1	FP	729	723	1452
122	f	2	AL	985	995	1980	225	f	3	FP	555	581	1136
123	f	2	AL	989	1010	1999	227	f	3	FP	380	416	796
124	f	3	AL	1008	1021	2029	228	f	2	FP	506	571	1077
127	f	1	AL	198	221	419	234	f	2	BI	1160	1247	2407
129	f	4	AL	946	955	1901	236	f	4	BI	1140	1237	2377
131	f	3	BI	964	1014	1978	238	f	5	BI	343	389	732
132	f	2	BI	910	890	1800	239	f	3	FP	1168	1255	2423
133	f	3	BI	876	844	1720	240	f	4	BI	1112	1182	2294
134	f	2	BI	592	549	1141	241	f	4	BI	226	274	500
135	f	3	BI	97	112	209	242	f	4	BI	1158	1245	2403
136	f	3	BI	84	99	183	243	f	4	AL	1160	1247	2407
138	f	3	BI	349	352	701	248	f	4	BI	1162	1248	2410
139	f	3	AL	475	452	927	251	f	4	BI	1165	1252	2417
144	f	3	AL	1004	1014	2018	259	f	4	FP	1151	1241	2392
145	f	2	BI	1006	1025	2031	261	f	3	BI	114	153	267
146	f	3	BI	798	758	1556	262	f	4	FP	1163	1249	2412
147	f	1	BI	1006	1002	2008	263	f	5	BI	1001	1019	2020
150	f	1	BI	1005	1019	2024	264	f	4	BI	264	311	575
151	f	2	BI	1003	1016	2019	269	f	4	BI	302	353	655
152	f	3	BI	898	892	1790	271	f	3	BI	649	635	1284
153	f	3	BI	1008	1023	2031	277	f	3	FP	1163	1230	2393
156	f	2	BI	1010	1018	2028	278	f	1	AL	1169	1263	2432
163	f	2	BI	1003	1019	2022	280	f	3	BI	1173	1262	2435
164	f	2	BI	932	988	1920	286	f	5	BI	163	182	345
165	f	2	AL	1002	1021	2023	287	f	3	AL	263	298	561
167	f	2	BI	467	453	920	288	f	5	BI	93	115	208
168	f	3	BI	597	551	1148	290	f	1	AL	1243	1094	2337
171	f	2	BI	1008	1023	2031	292	f	2	BI	872	777	1649
177	f	3	BI	225	249	474	295	f	2	BI	1174	1019	2193
180	f	2	BI	1005	1032	2037	296	f	2	BI	1231	1035	2266
183	f	3	AL	1008	1025	2033	301	f	4	AL	1235	1098	2333
184	f	5	AL	1006	1035	2041	305	f	3	BI	1296	1083	2379
185	f	3	BI	150	171	321	307	f	5	BI	1153	1231	2384
188	f	1	BI	1002	1025	2027	310	f	3	AL	1207	1094	2301
194	f	3	AL	1010	1020	2030	311	f	1	AL	1280	1071	2351
195	f	3	AL	906	892	1798	314	f	5	AL	111	137	248
200	f	3	BI	983	982	1965	318	f	4	FP	868	909	1777
201	f	1	BI	1014	1022	2036							

Table 3.4. Population-level selection coefficients and 95% credible intervals for each habitat variable, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

Veg. Assoc.	**Lower 95% CI**	**Mean**	**Upper 95%CI**
Cypress	-6.26E-03	3.99E-04	8.56E-03
Flatwoods	-5.77E-03	1.74E-03	1.17E-02
Hammock	-3.86E-03	-5.68E-05	3.94E-03
Marsh	-1.30E-02	1.55E-03	1.91E-02
Prairie	-3.75E-03	6.42E-04	6.98E-03
Edge	-1.30E-02	8.89E-04	1.49E-02
ORV Trail	-4.13E-03	7.02E-05	4.28E-03

Table 3.5. Model selection table provides results for each spatial covariate included in resource selection analyses with degrees of freedom, AICc score, delta AICc, and model weight, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

Model	**df**	**AICc**	**ΔAICc**	**AICc Weight**
Cypress				
Depth + Time	5	-20079.7	0	0.63
Time	4	-20078.6	1.07	0.37
Road				
Time	4	-22825.3	0	0.91
Time + Depth	5	-22820.7	4.61	0.09
Prairie				
Null	3	-21547.1	0	0.997
Depth	4	-21534.1	13.03	0.001
Edge				
Depth	4	-16939.4	0	0.74
Depth + Season	9	-16937.3	3.05	0.26
Marsh				
Depth:Sex + Depth:Site + Season:Time	21	-16545.8	0	1
Depth:Site + Season:Time	19	-16534.6	11.21	0
Flatwoods				
Depth + Time	5	-18857.9	0	0.92
Depth	4	-18853.1	4.79	0.08
Hammock				
Depth	4	-22921.5	0	0.83
Null	3	-22918.4	3.16	0.17

Table 3.6. Model selection table provides results for linear mixed models estimating the effects of depth, site, season and sex on home range and core are sizes including degrees of freedom, AICc score, delta AICc and model weights, Big Cypress Basin, Florida, 1 February 2015 – 1 February 2017.

Model	**df**	**AICc**	**ΔAICc**	**AICc Weight**
Home Range				
Depth + Site + Season:Sex	17	3914	0	0.297
Depth:Site + Season:Sex	19	3914.7	0.7	0.21
Depth:Site + Season:Sex + Depth:Sex	20	3915.6	1.6	0.132
Site + Season:Sex + Depth:Sex	18	3915.9	1.9	0.115
Core Area				
Depth:Site + Season:Sex + Depth:Sex	20	4206.2	0	0.452
Season:Sex + Depth:Sex	18	4207.9	1.7	0.186

CHAPTER 4

CONCLUSIONS, IMPLICATIONS, AND FUTURE RESEARCH

White-tailed deer (*Odocoileus virginianus*; hereafter, deer) populations encounter a diverse array of biotic and abiotic factors that influence when and where individuals allocate time and energy to obtain resources for survival and reproduction (Stewart et al. 2011). I found evidence that regional hydrology and risk of predation by Florida panthers (*Puma concolor coryi*) influence activity patterns, resource selection, and space use of deer in the Big Cypress Basin of southwestern Florida. With combined results from the analysis of detection rates and activity overlap at camera traps and spatial resource selection analysis at multiple temporal scales, I conclude that 1) deer recognize spatial and temporal variability in risk of predation and behaviorally mitigate exposure to high risk, 2) the local hydrological regime is a significant driver of deer space use, and 3) hydrology may interact with risk of predation by limiting resource availability and morphing of the landscape of fear (Laundré et al. 2001) such that deer much expose themselves to greater risk to acquire adequate forage.

Deer reduced activity in places and at times characterized as high-risk by high panther detection rates. Detections rates of panthers at camera traps positioned on off-road vehicle (ORV) trails exceeded those at off-trail locations by up to 875% and nocturnal detections substantially outnumbered diurnal. I documented aversion to deer activity in high-risk scenarios as deer apparently reduced exposure to risk by decreasing activity during nocturnal hours, particularly in the vicinity of ORV trails. I demonstrated that the sexes of deer respond differently to risk of predation as male activity generally exceeded that of females in high-risk scenarios (e.g., on-trail at night), suggesting that males and females employ different anti-predators strategies. Moreover, the sexes engaged in their most risk prone behavior during periods of respective reproductive importance when energetic demands peaked. Females increased exposure to risk during the fawning and fawn-rearing seasons while male exposure to risk peaked during the pre-rut and rut seasons providing support for the hypothesis that sex-specific energetic demands of reproduction interact with risk of predation to drive sexual segregation in polygynous ungulates.

In contrast to my activity patterns results, I documented minimal differences in resource selection of the sexes over a broader timescale that included two consecutive years, one relatively dry and one witnessing a record-setting flood event. Linear models indicated no effect of sex on selection of habitat variables, which may be a result of increased similarity in resource use as a function of limited resource availability, as mean surface water depth contributed significantly to variability of selection of every habitat category except prairies. Contrary to the results of Miller (1993) and Sargent (1992), I provided evidence of shifts in selection of habitats that correlated strongly with mean surface water levels, which corroborates the findings of MacDonald-Beyers and Labisky (2005). Selection of pine flatwoods, a vegetation community associated with relatively dry sites, correlated positively with mean surface water levels while selection for flood prone marshes correlated negatively with water depth. The similarity of selection by the sexes suggests that limited resource availability attributed to widespread inundation reduces sexual segregation in deer of the BCB. Limited availability may also explain positive correlation of male and female home range size with mean surface water levels, however an effect of water depth on male core area size with no effect on female core area size suggests that limited resources place a greater strain on males. This notion supports the reproductive-strategy hypothesis, also called the predation risk hypothesis by Ruckstuhl and Neuhaus (2000), for sexual segregation. The reproductive-strategy hypothesis predicts that males will seek greater abundances of forage while females will maintain stronger fidelity to reliable resources (Main et al. 1996). Resource selection results provided further support for the reproductive-strategy hypothesis by demonstrating that differences in sex-specific selection peaked during the fawning and rearing seasons when the sexes should be most segregated. However, a decreased differential in resource selection by the sexes during the wet 2016 fawning and rearing seasons suggests an interplay between hydrology and risk of predation as the reproductive-strategy hypothesis also predicts selection of the safest habitat for neonates that provides adequate resources to females during this time (Main et al. 1996).

I further evaluated the effects of risk of predation on space use under a resource selection framework by including spatial features potentially associated with high risk, forest edge and ORV trails. While I documented minimal selection for use of trails, deer only selected for trails during low-risk, diurnal hours and only during high-water events. Conversely, deer selected against forest edges, which conceivably provide concealment cover for panthers, during high-risk nocturnal hours of dry periods. However, deer selected for forest edges during periods of elevated surface water levels but only during low-risk diurnal hours. Additionally, high-risk, nocturnal selection for marshes by females in the dry 2015 fawning season may indicate that females perceived marshes as low-risk habitats. Subsequent avoidance of marshes during the wet 2016 fawning season suggests that hydrology interacts with risk of predation by either forcing reevaluation of predation risk and shifting the landscape of fear or imposing a risk of starvation that supersedes risk of predation (Kie 1999).

In the BCB, risk of predation represents an ever-present constraint factoring into optimal foraging. Avoidance of preferred panther travel corridors (ORV trails) during times when they are most heavily utilized by panthers (night) supports the idea that fear influences the spatiotemporal distribution of deer (Laundré et al. 2001). However, seasonal flooding appears to impose a greater constraint on energetic intake via reduction of available resources, thus re-weighting the relative importance of predation risk in behavioral decision-making (Lima and Dill 1990). My results warrant further investigation of the extent to which ORV trails affect deer in the BCB as other studies have demonstrated adverse consequences for prey species in the context of anthropogenic corridors (Stuart-smith et al. 1997; James and Stuart-Smith 2000; Whittington et al. 2011; DeGregorio et al. 2014). Additionally, extreme flood events appear to force deer to utilize less preferable, or even avoided, vegetation communities and spatial features, which potentially expose them to an elevated risk of predation. Increased utilization of limited habitat may also adversely affect plant communities as population densities of deer in the vicinity of the limited available resources likely increases. Thus, rapid anthropogenic removal of standing water from the landscape via pump stations following extreme flood events may reduce the duration of exposure of deer to elevated risk of predation and reduce habitat degradation resulting from increased herbivory in limited areas of resource availability. However, given the atypical, extreme hydrological event that occurred during the second year of my resource selection study, I encourage managers to exercise caution in implementing habitat management plans based on previously discussed resource selection results until ongoing remote monitoring of deer in the BCB is complete.

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