WHITE-TAILED DEER, COYOTES, AND THE ECOLOGY OF FEAR IN A LONGLEAF PINE SAVANNA

By

MICHAEL JOHN CHERRY

(Under the Direction of Robert J. Warren)

Abstract

Predators can exert powerful influence on their prey, independent of direct killing, by inducing antipredator responses. Coyotes (*Canis latrans*) have recently achieved abundances capable of influencing white-tailed deer (*Odocoileus virginianus*) population demography in the southeastern USA, but the effects of antipredator responses have not been reported. I conducted a multifaceted investigation of coyote and white-tailed deer interactions, using population monitoring data, harvest data, and results from controlled experimentation with predator exclosures. This work provided evidence that coyotes can influence white-tailed deer space use and vigilance while foraging, and documented a negative relationship between coyote abundance and body mass of adult female deer during an 11-year period. I compared multiple measures of reproductive success during a 7-year period that encompassed high and low coyote-deer ratios to elucidate the relative contributions of direct predation and predation risk effects to an observed increase on recruitment as measured by fawn-adult female ratios. Fawn survival rates were similar between periods, but the proportion of females with evidence of ovulation increased during the period of low coyote-deer ratios. Increases in ovulation were similar to increases in the proportion of females with evidence of lactation and fawn-adult female ratios. While direct killing by predators greatly influenced survival of fawns during both periods, changes in recruitment resulted from variations in fecundity. I tested hypotheses predicting the consequences of 10 years of predator exclusion on oak (*Quercus* sp.) recruitment and the density of selected deer forage species. Oaks are an important component of the longleaf pine savannas, and factors influencing their recruitment are of significant importance to the restoration and management of the longleaf pine (*Pinus palustrus*) ecosystem. Predator exclusion increased oak recruitment and decreased the density of selected deer forage species in a frequently burned longleaf pine savanna. Thus, coyote predation risk can influence white-tailed deer herbivory and thereby potentially affect composition of groundcover and hardwood understory in longleaf pine ecosystems. This study demonstrates that coyotes can have strong predation risk effects on white-tailed deer populations, and ignoring these effects may result in dramatic underestimation of impacts of expanding coyote populations on ecosystems.

Index words: Body mass, coyote, *Canis latrans*, fecundity, herbivory, longleaf pine, non-consumptive effects, *Odocoileus virginianus* predation risk effects, recruitment, trophic cascade, vigilance, white-tailed deer

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MICHAEL JOHN CHERRY

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MICHAEL JOHN CHERRY

Major Professor:	Robert J. Warren
Committee:	L. Mike Conner
	Nathan P. Nibbelink
	Lindsay R. Boring

Electronic Version Approved:

Julie Coffield
Interim Dean of the Graduate School
The University of Georgia
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DEDICATION

I dedicate this dissertation to my wife, Taulbee, and son, John Russell, for providing the right amount of motivation and distraction throughout the process.

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CHAPTER 1

INTRODUCTION, LITERATURE REVIEW, STUDY AREA, OBJECTIVES, AND DISSERTATION FORMAT

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) populations face considerable variation in predation rates across the species' range. In the southeastern USA, biologists managed white-tailed deer herds with little consideration of predation until the relatively recent colonization of the region by coyotes (*Canis latrans*). There has been much effort allocated to quantify the effects of coyotes on white-tailed deer population demography in the Southeast, but predicting the occurrence and magnitude of predator effects remains elusive. Thus biologists are often left rendering management decisions or providing landowners recommendations with great uncertainty, and inadequate information regarding local predator-prey dynamics.

Several lines of evidence suggest coyotes reduce fawn recruitment in the Southeast, including coyote removal studies (Howze et al. 2009, Van Gilder et al. 2009), and fawn survival data (Bowman et al. 1998, Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, McCoy et al. 2013, Nelson 2013), and coyote diet studies (Stratman and Pelton 1997, Schrecengost et al. 2008, Grigione et al. 2011, McVey et al. 2013). However, predators can influence their prey through two pathways: (1) direct predation, and (2) by eliciting antipredator responses. Previous studies of predator-prey dynamics have focused solely on the effects of predators killing their prey, but there is a growing appreciation for the behavioral interactions between predators and their prey, and the subsequent effects of these interactions on prey populations.

In classic models of predator-prey population dynamics (Rosenzweig and MacArthur 1963, Murdoch and Oaten 1975), predators influence prey population size, but these models do not consider the behavioral response of prey, which can cause significant deviations between model predictions and reality. Foraging theory predicts that prey species will balance competing demands for food and safety by allocating time among safe and risky habitat patches, and increasing vigilance during risky conditions (MacArthur and Pianka 1966, Sih 1980, Lima and Dill 1990). Brown et al. (1999) combined the models for predator-prey population dynamics (Rosenweig and Mac Arthur 1963) with the foraging theory (MacArthur and Pianka 1966) and described the “ecology of fear,” defined as “the melding of the prey and predator's optimal behaviors with their population and community-level consequences.” The ecology of fear demonstrates how sophisticated behavioral interactions of predators and prey can explain empirical observations and provide feedbacks that buffer a predator-prey system.

Non-consumptive effects of predators on prey demography can be greater than consumptive effects (Preisser et al. 2005). Predators can have powerful non-consumptive effects on their prey by inducing behavioral (Hunter and Skinner 1998, Creel et al. 2005, Winnie and Creel 2007), physiological (Lima 1998; Clinchy et al. 2004, 2013; Travers et al. 2010), and morphological (Banks et al. 1999, Tollrian and Harvell 1999, Vamosi and Schluter 2004) responses. These antipredator responses have activity costs that may influence prey demography if they decrease birthrates or increase susceptibility to other morality factors (Creel and Christianson 2008). The costs associated with antipredator responses can reduce fecundity of numerous free-ranging vertebrate species (Boonstra et al. 1998, Olaf and Halle 2004, Creel et al. 2007, Zanette et al. 2011).

LITERATURE REVIEW

Coyotes and White-tailed Deer

White-tailed deer evolved as a prey species adapted for complex interactions with their predators (Mech and Peterson 2003, Ballard 2011). The effect of predation on population demography and growth depends on the state of the deer population. Consider the logistic population growth curve where the inflection point represents the highest rate of growth, and is the point after which the rate of population growth begins to decline. The inflection point occurs somewhere below the equilibrium or carrying capacity (K). If the population is situated to the left of the inflection point on the logistic growth curve, then predation is likely additive because resource-dependent mortality is low and survival is high. Conversely, if the population is situated to the right of the inflection point, then predation is likely a compensatory mortality source because resource-dependent mortality is high and survival is low (Ballard et al. 1999). Predicting the effects of predation on white-tailed deer population growth requires an understanding of how resources and environmental conditions influence fecundity and survival, as well as the complexities of predator-prey interactions.

During the latter half of the 20th century coyotes colonized many eastern USA ecosystems that lacked apex predators and associated top-down regulation for decades (Hill et al. 1987, Gompper 2002). Coyotes are now the largest predator native to North American that thrives in fragmented landscapes of the eastern USA, and understanding their specific effects on ecosystems is a high priority for guiding informed management. In addition to influencing white-tailed deer abundance and behavior (Lingle and Pellis 2002; Kilgo et al. 2010, 2012), coyotes can cause cascading effects to lower trophic levels through competitive exclusion of smaller predators (Sovada et al. 1995, Crooks and Soulé 1999, Henke and Bryant 1999). In the absence of apex predators, coyotes can exert strong top-down influences on ecosystems that range from increasing mammalian (Henke and Bryant 1999) or avian (Crooks and Soulé 1999) diversity to causing the declines in species of concern (Ripple et al. 2013). The effects of coyote predation on white-tailed deer are highly variable; perhaps because coyotes display tremendous phenotypic plasticity across their distribution and can occupy multiple ecological niches.

Coyotes are capable of preying on large cervids including moose (*Alces alces*; Benson and Patterson 2013) and are known predators of adult white-tailed deer (Whitlaw et al. 1998, Patterson and Messier 2003). Lingle and Pellis (2002) reported coyotes preferentially preyed upon larger mule deer (*Odocoileus hemionus*) over sympatric white-tailed deer. However, most studies identifying coyotes as significant predators of adult white-tailed deer occurred in northern temperate climates where predators are aided during winter by deep snow and reduced body condition of white-tailed deer (Ballard 2011). Patterson and Messier (2000) reported that ecological factors such as deer abundance, alternative prey abundance (i.e., snowshoe hare *[Lepus americanus*]), and vulnerability due to winter severity better predicted killing rates of deer by coyotes, than predator-prey ratios. Patterson and Messier (2003) demonstrated that the femur marrow fat reserves of deer killed by coyotes did not differ from deer killed by deer-vehicle collisions, and on one site, fawns were disproportionally preyed upon, but on another site the age distribution of white-tailed deer killed by coyotes was similar to the age distribution of samples from deer-vehicle collisions. These finding are in contrast with the predator-sensitive foraging hypothesis put forth by Sinclair and Arcese (1995). This hypothesis suggests that prey should take greater risks to acquire resources as nutritional condition decreases and, therefore, predators should disproportionally prey on individuals in poorer nutritional condition. Patterson and Messier (2003) suggest severe winter conditions likely compromised the ability for white-tailed deer to evade coyotes, resulting in a lack of selection for young, sick, weak, and old individuals. In the southeastern USA where there is an absence of severe winter conditions, coyotes can prey heavily on white-tailed deer fawns (Kilgo et al. 2012 and many others), and some evidence exists for predation on pregnant adult females (Chitwood et al. *in press*), but I am unaware of any study describing coyotes as a significant mortality source for adult white-tailed deer in this region.

Kilgo et al. (2010) offered multiple lines of evidence suggesting coyotes may be impacting deer populations in South Carolina and likely throughout the Southeast. Howze et al. (2009) and Van Gilder et al. (2009) conducted predator removals on properties in Georgia and Alabama, respectively, and demonstrated predators were limiting white-tailed deer recruitment on those sites. Fawn mortality rates are highly variable across the USA (Table 1.1). In general, fawn mortality is greater in in the Southeast than the Midwest. However, comparing across studies can be problematic because the probability of fawn survival increases with age, and these researchers used various capture methods, which can result in variation in fawn age at capture. For example, two recent studies from South Carolina are difficult to compare because McCoy et al. (2013) reported a mean age at capture of 7.24 ± 0.16 days, whereas Kilgo et al. (2012) captured 81% of their sample within hours of birth, but they do not provide age at capture estimates for the remaining 19% of their fawns. Kilgo et al. (2012) reported 77% mortality compared to 32% by McCoy et al. (2013); however, it is difficult to separate the effects of study site and capture method (i.e., age) used in these two studies on fawn survival. Monitoring radio-marked fawns provides evidence of the causes of mortality, which can lead to a mechanistic understanding of factors influencing recruitment. In the Southeast coyote predation is often the primary source of mortality for white-tailed deer fawns (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, McCoy et al. 2013).

White-Tailed Deer Nutrition and Reproduction

As an iteroparous capital breeder, deer must balance the energetic costs of reproduction with body growth and maintenance to ensure future productivity. If nutritional costs of previous reproductive efforts are not recouped before the next breeding season, then capitol breeders may forgo reproduction (i.e., reproductive pause; Cameron 1994) or reduce maternal investment (Therrien et al. 2007, 2008; Taillon et al. 2013). White-tailed deer fecundity is sensitive to factors that influence nutritional condition, such as population density and environmental factors (Rhodes et al. 1985, Mech et al. 1987, Simard et al. 2014). However, ovulation itself is not an energetically demanding process, which suggests that decreased nutritional condition likely reduces fecundity through physiological processes that decrease or delay reproductive investment (Bronson and Manning 1991). Litter size is influenced by nutritional condition. Healthy deer populations average 1.6-1.8 fawns per adult female, but resource limitation reduces productivity (Verme 1965, 1967; Rhodes et al. 1985; Ditchkoff 2011).

Body mass is a common metric used for monitoring health and fecundity in cervid populations (Verme 1967, Sæther and Haagenrud 1983, Cameron et al. 1993, Hewison 1996, Pettorelli et al. 2002, Cook et al. 2004). Body mass and condition have been linked to fecundity in deer (Verme 1967, Strickland et al. 2008), but causative inference is difficult from these data alone because body mass and reproduction influence each other (Festa-Bianchet et al. 1998, Strickland et al. 2008, Simard et al. 2014). In other words, body mass influences fecundity positively, but gestation and particularly lactation influence body mass negatively. Body mass fluctuates in female ungulates through the reproductive cycle and relatively high or low body mass may have different implications for reproduction, depending on the timing of the sample relative to reproductive chronology. For example, during the first month post-partum when energy requirements for female ungulates increase 65-215% (Oftedal 1985, Parker et al. 2009), females that are in the best nutritional condition are likely to be the individuals that did not reproduce. Therefore, depending on reproductive chronology, greater body mass may represent low fecundity. However, during the breeding season females in the best nutritional condition are likely to have larger litters, which demonstrates that greater body mass may also represent greater fecundity (Ditchkoff 2011). Annual variation in body mass may have multiple potential implications for fecundity as well. For example, if a manager increases forage availability for deer, then increases in body mass are possible; however, if reproductive investment subsequently increases, then body mass may be similar or decrease following land improvements, due to the energetic investment in reproduction. Body mass is an informative metric representing herd nutritional condition, but must be accompanied by age and reproductive condition data to be interpreted correctly.

Young deer must balance energetic demands for reproduction and growth and, therefore, body mass and condition in young cohorts are more susceptible to environmental factors than older age cohorts (Gaillard et al. 2000, Strickland et al. 2008). Resource conditions experienced while in utero are related to adult body mass of red deer (*Cervus elaphus*: Albon et al. 1992) and white-tailed deer (Mech et al. 1991). Annual variation in resource availability can result in variation in body mass among cohorts of white-tailed deer (Gaillard et al. 2003). Cohort effects can persist through life (Albon et al. 1992) and potentially across generations (Mech et al.1991), but the strength and duration depend on resource availability. When adequate resources are available, red deer and white-tailed deer can compensate for decreased juvenile size and overcome cohort effects during adulthood (Post et al. 1997, Strickland et al. 2008).

Predation Risk Effects

Predators affect prey populations via 2 pathways—(1) directly through killing and (2) indirectly through sublethal interactions (Werner and Peacor 2003). In some cases, the indirect effects of predation can be more important than direct effects on prey populations (Preisser et al. 2005) and food web dynamics (Ripple and Bescheta 2004, Schmitz et al. 2004). Prey response to predation risk can be morphological (Banks et al. 1999, Tollrian and Harvell 1999, Vamosi and Schluter 2004), behavioral, (Hunter and Skinner 1998, Creel et al. 2005, Winnie and Creel 2007) or physiological (Boonstra et al. 1998; Lima 1998; Clinchy et al. 2004, 2013; Sheriff et al. 2009). The cumulative costs associated with prey responses can affect fecundity and reproduction (Olaf and Halle 2004, Creel et al. 2007, Travers et al. 2010, Zanette et al. 2011).

Foraging tradeoffs between safety and resources are the foundation of the study of predation risk effects (MacArthur and Pianka 1966, Sih 1980, Brown et al. 1999). . Peckarsky et al. (2008) demonstrated that the inclusion of predation risk effects provided new insights to textbook examples of predator-prey systems. By embedding foraging theory in population models, Brown et al. (1999) resolved deviations between models and observations, and demonstrated how behavioral responses buffer predator-prey systems. For example, decreased predator densities and predation risk would yield less vigilant and more catchable prey, resulting in increased individual predator fitness and fecundity, even when prey are rare and abundance is limited by factors other than predation. This concept was expanded into a spatially explicit context by Laundre et al. (2001) who suggested the effects of predator-prey interactions and their implications for population- and community-level consequences, likely vary through space creating a "landscape of fear." The landscape of fear concept suggests that biotic and abiotic factors distributed across a landscape influence predation risk perceived by prey, resulting in spatial heterogeneity in behavior and associated consequences. In this conceptual landscape the topography represents variation in perceived predation risk, and understanding the causes of topographic variation may provide spatially explicit predictions for variation in prey fitness and impacts on food web dynamics.

Ungulates often respond to predation risk by altering vigilance rates (Hunter and Skinner 1998, Laundre et al. 2001, Winnie and Creel 2007), habitat selection (Creel et al. 2005, Thaker et al. 2011), and diet selection (Edwards 1983, Creel and Christianson 2009). Vigilance while foraging is a common measure of antipredator responses in ungulates, perhaps because it can be directly related to resource acquisition rates, and then by extension to prey fitness and impacts on lower trophic levels (Lima and Dill 1990, Brown et al. 1999, Laundre et al. 2001, Brown and Kotler 2004, Fortin et al. 2004). The optimal vigilance response should equilibrate along a gradient of opposing risks of starvation (or loss of fitness) and predation (Lima and Dill 1990, Brown et al. 1999). Ungulates alter habitat selection in response to predation risk (Edwards 1983, Creel et al. 2005, Thaker et al. 2011). Edwards (1983) documented moose reduced predation risk by using small islands, particularly during calving, despite poorer forage availability. Creel et al. (2005) demonstrated that the presence of gray wolves (*Canis lupus*) resulted in a reduced use of preferred grassland habitats and increased use of wooded habitats, presumably for increased cover. Shifts in habitat selection caused by predation risk can also result in altered diet composition. For example, Christianson and Creel (2008) demonstrated female elk (*Cervus elaphus*) decreased grazing during pulses of increased predation risk, and Creel and Christianson (2009) documented elk increased consumption of willow browse in response to predation risk. This shift in foraging behavior in elk from grazing to browsing is likely a function of increased use of forested cover in response to increased predation risk (Creel et al. 2005, Fortin et al. 2005).

Ecologists have long searched for generalizations describing traits of predators, prey or ecosystems that can predict the outcome of predator-prey interactions on food web dynamics. A theoretical framework predicting the strength and occurrence of predation risk effects on prey populations, communities and ecosystems is emerging (Preisser et al. 2007, Schmitz 2008, Creel and Christianson 2008, Heithaus et al. 2009, Creel 2012, Miller et al. 2014). Preisser et al. (2005) demonstrated predation risk effects tend to decrease with increasing resource limitation. Predator hunting mode has also shown promise in predicting predation risk effects (Preisser et al. 2007 Schmitz 2008, Miller et al. 2014). Theory predicts sit-and-wait and sit-and-pursue predators induce stronger non-consumptive effects than active hunting predators, because they provide more predictable risk cues. Extending this theory to large free-ranging vertebrates has yielded variable results. As an active hunting predator, wolves are predicted to have numeric, but weak behavioral effects on prey, however, wolves have induced strong effects on elk behavior (Winnie and Creel 2007), nutritional condition (Christianson and Creel 2010), and fecundity (Creel et al. 2007). However, others did not find evidence of predation risk effects on elk or lower trophic levels, which supports the predator hunting mode hypothesis (Kauffman et al. 2010, White et al. 2011, Winnie 2012, Middleton et al. 2013) Prey traits and landscape attributes may also predict the occurrence of predation risk effects (Heithaus et al. 2009, Creel 2012).

Physiological responses to predators can cause reduced prey survival and birthrates, providing an intuitive mechanism for predator effects on prey demography that is independent of direct killing of prey (Clinchy et al. 2013). The sight or smell of predators can cause measureable physiological responses in prey (Cockrem and Silverin 2002, Campeau et al. 2008) that can have long-lasting effects, even from a single exposure to a stressor (Adamec and Shallow 1993, Armario et al. 2008). Boonstra et al. (1998) demonstrated snowshoe hare population cycles were tied to decreases in fecundity that resulted from physiological stress induced by predation risk rather than stress caused by population density or decreased nutritionally mediated stress. Subsequently, Sheriff et al. (2009) documented a correlation between fecal cortisol metabolite and litter size, and offspring body mass in snowshoe hares. Traver et al. (2010) simulated nest predation on song sparrow nests and documented decreased clutch size in successive nesting attempts and poorer physiological condition.

Predator effects on prey fecundity can be substantial in a diverse group of species (Preisser et al. 2005; Creel et al. 2007, 2009; Travers et al. 2010; Zanette et al. 2011). Olaf and Halle (2004) applied a predator odor treatment to an area occupied by free-ranging grey-sided vole (*Clethrionomys rufocanus*) populations and documented a decrease in the proportion of reproductively active females and recruitment of juveniles relative to control populations. Sheriff et al. (2009) documented negative effects of a simulated predation risk treatment on snowshoe hare fecundity. The authors presented a non-lethal "predator" (i.e., a trained dog) to wild-caught snowshoe hares and documented reduced litter size and birth weights compared to a control group Zanette et al. (2011) exposed song sparrows (*Melospiza melodia*) to auditory predation risk cue and documented a 40% reduction in the number of offspring produced as a result of decreases in clutch sizes, egg hatchability, and nestling survival. The restoration of gray wolves in Yellowstone National Park, USA, caused elk to alter their vigilance (Laundre´et al. 2001, Winnie and Creel 2007), habitat selection (Creel et al. 2005), diet selection (Christianson and Creel 2008), and nutrient balance (Christianson and Creel 2010). These predator-induced behavioral changes were associated with reduced pregnancy rates and provided correlative evidence for predator-reduced prey fecundity (Creel et al. 2007).

Trophic cascades explain interactions between predators and the resources their prey consume (Paine 1980). There is growing evidence suggesting predators can exert powerful top-down effects on ecosystems by influencing prey abundance and behavior (Myers et al. 2007, Estes et al. 2011, Ripple et al. 2014). Trophic cascades often arise when predators indirectly protect plants by reducing herbivore abundance; however, behaviorally mediated trophic cascades (BMTCs) can occur when predators indirectly protect plants by altering foraging behavior of prey (Beckerman et al. 1997, Schmitz et al. 2004). Several observational studies have suggested BMTCs structure ecosystems following the restoration of large predators (Ripple and Beschta 2004, Fortin et al. 2005, Beyer et al. 2007, Beschta and Ripple 2009), but some have questioned the strength of trophic cascades in complex terrestrial systems and particularly when they involve behavioral interactions (Halaj and Wise 2001; Kauffman et al. 2010, 2013; Winnie 2012; Beschta and Ripple 2013). White-tailed deer herbivory has a tremendous effect on forested ecosystems (Stromayer and Warren 1997, Cote et al. 2004), but the influence of predators on those effects has received little attention (but see Callan et al. 2013).

In conclusion, white-tailed deer are a behaviorally sophisticated prey species with numerous behavioral adaptations that mitigate the risks of predators (Mech and Peterson 2003). Coyote colonization into the Southeast likely has induced antipredator responses in white-tailed deer, but these interactions have not been reported. Ecological theory suggests these interactions may have profound effects on white-tailed deer and food web dynamics. My dissertation research was designed to examine coyote-white-tailed deer interactions in a longleaf pine (*Pinus palustrus*) savanna as a basis for evaluating the potential for coyote predation risk effects on white-tailed deer and their trophic level interactions.

STUDY AREA

My research took place on Ichauway, the 12,000-ha outdoor research site of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia, USA. Ichauway included approximately 7,250 ha of longleaf pine stands. Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens–Nyssa biflora*) limesink ponds (Boring 2001). Management on Ichauway followed the Stoddard-Neel approach to ecological forestry, which emphasizes balancing multiple objectives, rather than maximizing the production of any one amenity (Mitchell et al. 2006). Prescribed fire was the primary management tool used to maintain the longleaf pine ecosystem on Ichauway.

Longleaf pine-wiregrass (*Aristida stricta*) savannas of the southeastern USA are characterized by globally significant levels of biodiversity, with numerous endemic species of flora and fauna (Peet and Allard 1993, Mitchell et al. 2006). As many as 50 plant species can occur in a single square meter, with >1,100 species on 11,000 ha (Drew et al. 1998, Kirkman et al. 2001). A frequent (e.g. often 1-3 years) fire-return interval increases species richness by maintaining an open canopy, virtually absence midstory, and a diverse groundcover (Glitzenstein et al. 1995, Kirkman et al. 2004). Many fire-impeding tree species exist in a “fire trap,” or demographic bottleneck where they repeatedly sprout after loss of aboveground biomass, but rarely escape into older size classes due to frequent fire (Grady and Hoffmann 2012). When fire-impeding species escape the fire trap, the midstory closes, floral and faunal diversity decrease, and fire becomes less frequent and more severe (Kirkman et al. 2004; Mitchell et al. 2006, 2009; Grady and Hoffman 2012). Oak encroachment to the midstory of longleaf pines stands adversely affects threatened and endangered species including the red-cockaded woodpecker (*Picoides borealis*) and gopher tortoise (*Gopherus polyphemus*; Walters 1991, Allen et al. 2006, Mitchell et al. 2006).

White-tailed deer abundance on Ichauway was managed through adaptive harvest to maintain densities well below carrying capacity to maximize herd health and minimize herd effects on the ecosystem. Estimated white-tailed deer densities were between 3.8-5.8 deer/km^2 during the study (B. Rutledge, personal communication). Coyotes and bobcats (*Lynx rufus*) were the primary non-human predators of white-tailed deer on my study area (Howze et al. 2009).

OBJECTIVES

I conducted a multifaceted investigation into the potential for coyote predation risk effects on white-tailed deer and their trophic interactions using long-term monitoring data, harvest data, and controlled experimentation to address the following objectives:

1) Evaluate the influence of predation risk on white-tailed deer space-use.
2) Examine the effects of coyote abundance on white-tailed deer body mass.
3) Investigate the sex-specific effects of predator exclusion on white-tailed deer vigilance, while concurrently examining the effects of group dynamics and season.
4) Evaluate the effect coyote predation risk on white-tailed deer reproduction independent of direct killing.
5) Examine effects of predator-mediated foraging behavior on plant communities in a longleaf pine savanna.

DISSERTATION FORMAT

This dissertation is presented in manuscript format. Chapter 1presents the introduction and literature review relevant to topics discussed in this dissertation. Chapter 2 presents two lines of data demonstrating the potential for coyote predation risk effects on white-tailed deer: (1) results of an eight-year experiment demonstrating predator exclusion influences white-tailed deer site selection, and (2) coyote abundance was an informative parameter in models predicting adult female white-tailed deer body mass during an 11-year period. Chapter 3 reports the results of an experiment using camera traps to investigate the sex-specific and seasonal effects of predator exclusion on white-tailed deer foraging behavior, while also evaluating the effects of group size and composition. Chapter 4 combines population monitoring data, white-tailed deer nutritional condition data, multiple measures of adult female deer reproductive condition, survival of marked fawns, and hunter observation data to elucidate the relative contributions of direct and indirect effects of predation on white-tailed deer recruitment. Chapter 5 reports results from an experiment investigating how predator exclusion may influence plant communities through altered food web dynamics. Chapter 6 provides conclusions and management implications.

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Table 1.1 Observed mortality rates, sample sizes, and study location from previous white-tailed deer fawn mortality studies in North America (1971-2013).

Study	Year	Location	# of fawns	Mortality rate (%)
Cook et al.	1971	TX	81	71.6
Garner et al.	1976	OK	35	82.9
Carroll and Brown	1977	TX	120	40.8
Bartush and Lewis	1981	OK	48	90.0
Epstein et al.	1985	SC	45	84.4
Huegel et al.	1985	IA	55	23.6
Nelson and Woolf	1987	IL	54	30.0
Sams et al.	1996	OK	76	38.2
Whittaker and Lindzey	1999	CO	37	64.9
Brinkman et al.	2004	MN	39	15.4
Vreeland et al.	2004	PA	218	48.6
Burroughs et al.	2006	MI	75	22.6
Roberts	2007	SC	134	78.4
Saalfeld and Ditchkoff	2007	AL	36	66.7
Rohm et al.	2007	IL	166	41.0
Kilgo et al.	2012	SC	91	77.0
Jackson and Ditchkoff	2013	AL	14	74.0
McCoy et al.	2013	SC	210	32.0
Nelson	2013	GA	47	71.0

CHAPTER 2

PREDATION RISK EFFECTS ON WHITE-TAILED DEER SITE-SELECTION AND BODY MASS[1]

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[1] Cherry, M. J., L. M. Conner, B. T. Rutledge, and R. J. Warren. Submitted to *PLOS ONE* 5/26/2014

ABSTRACT: Predators affect prey populations through direct predation, and through the costs of antipredator responses. Non-consumptive effects (NCEs) occur when antipredator responses result in patterns at the population, community, or ecosystem levels. We studied the NCEs of coyotes (*Canis latrans)* on site-selection and body mass of white-tailed deer (*Odocoileus virginianus*) at the Joseph W. Jones Ecological Research Center, Georgia, USA. We determined site-selection by monitoring white-tailed deer use of 4, approximately 40-ha, fenced predator exclosures and 4 unfenced controls plots, using track count and thermal camera surveys from 2004-2011. Predator exclosure fences were readily crossed by white-tailed deer, creating prey refugia in a design where habitat structure and resource availability were standardized and only predator abundance varied by treatment. White-tailed deer detections were 2.1 times greater for track count surveys ($\chi2=73.74$ df=1, $P<0.001$) and thermal camera surveys ($\chi2=19.25$, df=1, $P<0.001$) in predator exclosures, experimentally demonstrating the influence of predations on site-selection of white-tailed deer. We used data collected from 476 adult (≥ 2.5 years of age) female white-tailed deer harvested during 1999-2011, to evaluate effects of coyote abundance on white-tailed deer body mass. Before considering coyote abundance, we conducted a model selection procedure to identify the best model predicting body mass as a function of individual and environmental variables. We then compared this best model to the best model plus the coyote abundance index to evaluate if the inclusion of the index improved predictive ability of the model. Coyote abundance was negatively related to female white-tailed deer body mass ($\beta=-1.22$ SE-0.55) and improved predictive ability of the model. We offer experimental evidence that the presence of exclosures influenced white-tailed deer site-selection and documented a negative relationship between coyote abundance and white-tailed deer body mass. Collectively our results support the hypothesis that coyotes have NCEs on white-tailed deer populations through behavioral interactions.

INDEX WORDS: Body mass, *Canis latrans*, coyote, non-consumptive effects, *Odocoileus virginianus,* predation risk, white-tailed deer

INTRODUCTION

Predators affect prey populations via two pathways— directly through mortality and indirectly through sublethal interactions [1]. Predators have non-consumptive effects (NCEs) when sublethal interactions result in change at population, community, or ecosystem levels. In some cases, indirect effects of predation can be more important than direct effects on prey populations [2], [3] and food web dynamics [4]-[6]. Prey response to predation risk can be morphological [7]-[9] behavioral, [10]-[12] or physiological [13]-[16], and the cumulative costs associated with prey responses can affect fecundity and reproduction [3], [15]-[19].

Prey species may restrict their use of or modify their behavior in areas of increased risk [11], [20], [21]. Laundre et al. [22] conceptualize the temporally dynamic spatial variation in predation risk as a "landscape of fear," a continuous gradient of perceived risk with patterns occurring at multiple spatial scales. Variation in risk can influence space-use of prey [22]-[25] because profitability of foraging in a patch is a function of net energetic intake counterbalanced by the incurred risk of predation [26].Therefore, if resources are constant, then prey should select patches with reduced predation risk. However, resources and risk are not homogeneous across most landscapes, which challenges foragers to balance competing demands for resources and safety, and creates the ecology of fear [26].

Many white-tailed deer (*Odocoileus virginianus*) populations in eastern North America occur without native predators (i.e., cougar [*Puma concolor*], red wolf[*Canis rufus*], and black bear [*Ursus Americana*]*;* [27]). In the absence of top-down suppression some white-tailed deer populations achieved densities incompatible with societal interests [28] and damaged ecosystem diversity and function [29]-[31]. White-tailed deer are highly interactive amongst trophic levels due to their susceptibility to effects of predation [32]-[34] and their ability to influence forest structure and ecosystems [35]-[37]. During the latter half of the 20th century coyotes (*Canis latrans*) colonized many ecosystems in the eastern USA that lacked non-anthropogenic, top-down regulation for decades [38], [39]. Coyotes are now the largest North American predator that thrives in much of the fragmented landscapes of the eastern USA, and understanding their specific effects on ecosystems is a high priority for guiding wildlife management efforts. Coyotes may induce cascading effects to lower trophic levels through competitive exclusion of smaller predators [40], [41] and through influencing herbivore abundance and behavior [32], [34], [42]-[44]. Coyotes are a highly interactive species [45], with an increasing abundance and range, which is capable of influencing white-tailed deer populations. The ecological importance of white-tailed deer demands an understanding of processes influencing foraging behavior and abundance to support informed management decisions [36].

Body mass can influence fecundity and is a common metric used for monitoring cervid populations [46]-[52]. Resource conditions experienced while in utero can influence adult body mass of red deer (*Cervus elaphus*: [53]) and white-tailed deer [54]. Annual variation in resource availability can lead to variation in body mass or fitness among cohorts [55]. Cohort effects can persist through life [53] and perhaps across generations [54], but the strength and duration depend on resource availability. When adequate resources are available, red deer and white-tailed deer can compensate for decreased juvenile size and overcome cohort effects during adulthood [56], [57]. We hypothesize that predators increase body mass of prey by decreasing lactation rates through direct predation, and decrease body mass of prey through NCEs. These mutually exclusive outcomes demonstrate why inference regarding fecundity is difficult with body mass data alone, and that NCEs of predators on prey body mass could be masked if analyses do not control for reproductive condition [58].

We hypothesize that coyote abundance influences white-tailed deer antipredator behaviors and that variation in antipredator responses alters white-tailed deer nutritional condition. Many studies have documented predator-mediated foraging in ungulates [10]-[12], [20], [32], but fewer have evaluated the cost of NCEs to nutritional condition, fitness, or population growth but see, [18], [59], [60]. To investigate antipredator behaviors of white-tailed deer, we conducted a 7-year experiment using predator exclosures that were permeable to white-tailed deer to measure the effects of predation risk on site-selection. To evaluate the effects of coyote abundance on white-tailed deer body mass, we compared models predicting body mass of female white-tailed deer harvested during an 11-year period using multiple environmental and individual variables with and without an annual coyote abundance index. We discuss the implications of NCEs on white-tailed deer populations in eastern USA.

MATERIALS AND METHODS

Study Site

Our study took place on Ichauway, the 12,000-ha research site of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia, USA. Ichauway included a heterogeneous mosaic of habitat types, surrounded by large-scale agricultural operations. The site included approximately 7,250 ha of longleaf pine (*Pinus palustrus*) stands. Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens*–*Nyssa biflora*) limesink ponds [61]. Approximately 10% (120 ha) of the site was cultivated wildlife openings and approximately 50% (6,000 ha) of the site was burned annually. White-tailed deer abundance was managed through adaptive harvest to maintain densities well below the nutritional carrying capacity to maximize herd health and minimize herd effects on the ecosystem. Estimated white-tailed deer densities were between 3.8-5.8 deer/km^2 during the study (B.T.R.., unpublished data). Coyotes were the primary non-human predator of white-tailed deer on our site [62]). On our site, bobcats rarely prey on deer and thus we assume they have minimal risk effects [63].

Predator Exclusion

In 2003 we chose 8, approximately 40-ha sites of similar habitat composition (i.e., longleaf pine-dominated canopy with native ground cover) to serve as study plots on a 2,025-ha portion of the Ichawauy. We randomly selected 4 plots to serve as mesopredator exclosures while the remaining 4 served as controls. At sites chosen for mesopredator exclusion, we constructed a 1.2-m high woven-wire (10X20–cm mesh) fence with electric wire attached to E2000 electrical fence chargers (Twin Mountain Fence Company, San Angelo, TX) along the top, middle, and bottom to deter mesopredators from climbing over or digging under fences. Predator exclusion plots were trapped using a combination of soft-catch (Woodstream Corp., Lititz, PA) and cage (Tomahawk Live Trap Company, Tomahawk, WI) traps. Trapping efforts targeted raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), grey foxes (*Urocyon cinereoargenteus*), red foxes (Vulpes vulpes), coyotes, and bobcats (*Lynx rufus*). Captured predators were relocated just outside the exclosure. To ensure the effectiveness of the treatment, sites were trapped twice annually for the duration of the study [64]. To control for effects of human disturbance, deer hunting, research, and management activities occurred across all exclosure and control plots. Predator exclosures were smaller than reported white-tailed deer home range estimates [65] and deer were frequently observed crossing fences. Additional details on our predator exclosures and their effectiveness in excluding coyotes can be found elsewhere [64], [66].

Predator Exclusion and Site-Selection

We used track count surveys [67] and thermal camera surveys [68] to monitor white-tailed deer abundance within exclosures and control plots. We monitored 5, 3 X 2-m track count stations per study plot along the inside edge of each exclosure and on perimeter roads of each control plot for 3 consecutive nights, twice seasonally from 2004-2011. We prepared track count stations by removing leaf litter and slightly disturbing the soil with a rake. No attractants or tracking surface materials were used on track count stations. Sandy soils on our study site provide an ideal tracking medium without introducing novel materials. We recorded an animal observation if we detected a track in the prepared surface. Thermal camera surveys were conducted from roads bordering the exclosure and control plots, 3 times per calendar season from 2004-2007. We mounted a PALM IR 250 thermal imager (Raytheon, Waltham, MA) in a research vehicle, then drove at approximately 15 km/hour around each plot and recorded the number of white-tailed deer observed within study plots. A primary objective of thermal camera surveys was to monitor the effectiveness of the predator exclusion treatment. We discontinued thermal camera surveys in 2007 once we were satisfied the treatment was effective at excluding mammalian predators and that track count surveys adequately captured variation in use among plots and through time. To determine if white-tailed deer disproportionally used the predator exclosures, we analyzed track count and thermal camera data separately using chi-square goodness-of-fit tests [69]. We maintained equal sampling effort within all plots and, therefore, expected white-tailed deer detections were equal within exclosures and controls. Thus, we used half of the total white-tailed deer observations for the expected value for both exclosure and control plots.

Coyote Abundance and Deer Body Mass

We used data from 476 adult (≥2.5 years old) female deer harvested on Ichawauy from 1999-2011to evaluate the effects predation risk on white-tailed deer nutritional condition. We used body mass as a surrogate for nutritional condition because it is a common metric used in population monitoring and has been related to fecundity and survival in numerous cervids [46]-[52].We used female deer for this modeling procedure because we hypothesized females would incur more antipredator costs associated with fawn-rearing and because variation in female nutritional condition is more likely to influence population level processes. Body condition and reproductive fitness of juvenile white-tailed deer is more sensitive to environmental conditions than adult age classes [57]. Therefore, our use of adult female white-tailed deer is a conservative approach because they are predicted to be more resilient to environmental change than juveniles [70]. We hypothesized that body mass of adult female white-tailed deer would be influenced by a combination of individual (i.e., date of harvest, age, reproductive condition), bottom-up (i.e., resource availability), and top-down (i.e., predation risk) factors, but our primary objective was to evaluate effects of temporal variation in coyote abundance on white-tailed deer body mass.

During the study, all legally harvested deer were brought to a check station where date, sex, body mass, age, and evidence of lactation were recorded. Age was estimated using tooth eruption and wear, and ranged from 2.5-6.5 years [71]. Based on preliminary analysis and small sample size of older age classes (i.e., 5.5 and 6.5 years), we categorized each white-tailed deer as 2.5, 3.5 or ≥4.5 years of age for analysis. To assign each white-tailed deer to a cohort, we subtracted the age estimate (2.5-6.5 years) from the year of harvest to identify the year of birth. Pregnancy and lactation are nutritionally demanding processes [72]; therefore, we documented evidence of lactation using palpation of utters. We used growing season precipitation (March-September) data from 2 National Oceanic and Atmospheric Administration weather stations on our site to calculate the total growing season rainfall for each year. Annual precipitation ranged from 44.9-113.2 mm and caused considerable variation in productivity of wildlife food plots and native forge (person communication; J. Atkinson, Land Manager). Because white-tailed deer lose body condition as they catabolize winter fat reserves [73], [74], we assigned each harvested animal a value ranging from 1-93 associated with the date of harvest (i.e., October 15=1 and January 15=93).

We developed indices of white-tailed deer and coyote abundance using detection data collected at 28 randomly distributed,1-km track count transects, monitored annually for 3 consecutive nights during July and August from 1999-2011. On our site, sandy roads provide an ideal tracking medium for observing occurrence of wildlife. Roads were prepared for surveys using 1 pass with a road grader and 2 passes with a road rake pulled behind a tractor. Between observations (i.e., daily) transects were cleared of all tracks using a chain drag implement pulled behind an all-terrain vehicle. The same observer monitored all transects in all years. The mean number of white-tailed deer and coyote detections per track count transect were calculated for each annual survey. Mean annual white-tailed deer and coyote detections per transect were 26.59 and 2.77 tracks per km respectively (Figure 1).

We used model selection to compare competing models explaining annual variation in body mass of adult female white-tailed deer. We explicitly excluded coyote abundance as a predictor and identified the best model predicting body mass of female white-tailed deer by comparing 22 models, including a null model, using combinations of variables representing individual and bottom-up forces (Table 1). We included random effects in all models to control for hunting season (12 classes) and cohort (16 classes) effects. We centered the mean to 0 of all continuous predictor variables for interpretation. We fit all linear mixed models using maximum likelihood and compared model fit and predicted variable importance using the second-order Akaike's Information Criterion (AIC*c*) and Akaike weights (w_i) [75], [76]. We calculated w_i to rank the set of models and interpreted the w_i as the probability of the ith model being the best model of the a priori set [75], [76]. We then compared this best model to the best model with the coyote abundance index to determine if the inclusion improved predictive ability of the model. The coyote abundance index would be considered an informative parameter if it improved the top model by >2 AIC_c points [76]. We developed parameter estimates, standard errors, and associated 95% confidence intervals for predictor variables included in the top model [76].

To accommodate those who prefer a hypothesis testing analysis to a model selection approach and for the sake of plurality of statistical approaches [77], [78], we used F-tests to test individual effects in the model including the coyote abundance index, using Satterthwaite approximation of degrees of freedom. We interpreted the importance of random effects using log likelihood ratio tests. Finally, we conducted a Pearson's Product-Moment correlation test of mean annual body mass of adult female white-tailed deer and annual coyote abundance index and report r^2 and P-values with alpha = 0.05. All analyses were conducted in program R 2.15, using package LMER.

Ethics Statement

All data were collected from white-tailed deer legally harvested by licensed hunters under Georgia state regulations. Trapping and monitoring was conducted under Georgia state wildlife collection permit 29-WJH-13-203.

RESULTS

Predator Exclusion and White-Tailed Deer Site-Selection

During 2004-2011, white-tailed deer were detected on track count stations more frequently ($\chi 2 = 73.74$ df = 1, $P < 0.001$) within predator exclosures than in control plots (404 and 194 detections, respectively). Similarly, white-tailed deer were detected during thermal camera surveys conducted 2004-2007, more frequently ($\chi 2 = 19.25$, df = 1, $P < 0.001$) in exclosures than in control plots (106 and 51 detections, respectively). White-tailed deer were detected 2.1 times more frequently in the exclosures than control plots using both monitoring methods.

Coyote Abundance and White-Tailed Deer Body Mass

We compared 22 models independent of a coyote abundance index predicting body mass at harvest of 476 adult (≥2.5 year old) female white-tailed deer harvested during 2000-2011. The best-fitting model included age (2.5, 3.5, or ≥4.5 years) and evidence of lactation (Table 2). To evaluate the effect of coyote abundance on white-tailed deer body mass we compared the top model without and with the coyote abundance index to determine if the inclusion improved predictive ability of the model (Table 3). The model including coyote abundance index was the best-fitting model with a w_i of 0.79 and reduced the AIC_c 2.7, providing support for coyote abundance as a predictor of female white-tailed deer weight. The best model predicting body mass of female white-tailed deer indicated that body mass was inversely related to coyote abundance index (β=-1.22, SE= 0.55) and evidence of lactation (β=-1.02, SE=0.53), and positively related to age (2.5 year [β= referent], 3.5 year [β= 2.84 SE=0.54] and 4.5 year [β= 2.88 SE=0.67]. The 95% confidence intervals contained 0 for all parameter estimates except age and coyote abundance (Table 4).

The hypothesis testing analysis provided similar results to the model selection approach, indicating coyote abundance index (P=0.045) and age (P≥0.001) significantly affected body mass (Table 5). We found no support for a cohort effect (X^2=4.55e^{-13}, P=1.0) and limited support for random annual variation (X^2= 2.45, P=0.06). The Pearson’s product-moment tests revealed a significant correlation between mean annual body mass of adult female deer and annual coyote abundance index (t=-2.54, df=10, P=0.029, Figure 2).

DISCUSSION

Collectively our results suggest coyotes can have profound NCEs on white-tailed deer populations. White-tailed deer were influenced by both temporal and spatial variation in coyote abundance. Our experimental design isolated the effect of predator abundance on white-tailed deer site-selection and accounted for any variation in resource availability in the random assignment of treatments. The balanced design allowed us to address site-selection, as plot types were equally available to the white-tailed deer population and disproportionate use would be considered selection. White-tailed deer selected sites where predators were excluded. We found body mass of adult female deer was negatively related to a coyote abundance index, and positively related to age, but not influenced by variables representing resource availability (i.e., deer abundance, growing season rain). We were able to experimentally demonstrate that predator exclusion influenced white-tailed deer site-selection, found evidence that coyote abundance affected white-tailed deer body mass, and speculated that these interactions may influence vital rates at the population level.

Observational evidence of predator-mediated prey behavior is abundant in the ecological literature (for review [79]). Much of our knowledge of NCEs is owed to “natural” experiments where predator distributions are heterogeneous across a landscape [80]-[82] however, lack of randomized assignment of treatments can facilitate inclusion of confounding effects into studies, thereby complicating interpretations [60], [83], [84]. Difficulty of implementing controlled experimentation increases with scale, and consequently experimentation at scales required to examine population-level behaviors and consequences are rare for large terrestrial vertebrates. By randomly assigning predator exclusion treatments to candidate plots with similar habitat composition, we controlled for the effects of resource availability on our conclusions and explicitly tested the effects of predator exclusion on white-tailed deer site-selection. Our results provide experimental support from a canid-cervid system for the predictions made by Brown et al. [26]—predators can influence abundance of prey in a patch through sophisticated behavioral interactions independent of direct predation.

We appreciate the importance of controlled experimentation for mechanistic understanding of processes and consider our results novel because of the scale and experimental control in investigation of a canid-cervid system. However, experimental results have limited utility if the observed patterns do not extrapolate beyond the treatment plots. Similarly, antipredator behaviors that do not induce NCEs have little ecological consequence. To investigate if the experimentally demonstrated behavioral process had NCEs at the population level, we used natural variation in coyote abundance over 12 years to predict body mass of adult female white-tailed deer. Our study is unique in that it used a large-scale controlled experiment to identify a behavioral process and long-term monitoring data to examine the potential effects of the process at the population level.

Our modeling efforts, hypothesis testing, and correlation tests indicated coyote abundance was negatively related to white-tailed deer body mass. These results suggest that increases in coyote abundance led to increased antipredator behaviors at the expense of white-tailed deer body condition. Our best model predicting body mass independent of coyote abundance included age and evidence of lactation as explanatory variables. The lack of predictive power of variables representing bottom-up forces (i.e., deer abundance index and growing season precipitation) in our best models may be a function of deer density relative to nutritional carrying capacity of our study area. Thus, supporting our prediction that the herd is maintained well below carrying capacity and even in years of low forage productivity, resources were not limiting. Hard mast production is critical to white-tailed deer nutrition in some systems [85], [86]. We did not include hard mast production in our modeling procedure because local data were unavailable, but we suggest there would have been minimal impact due to the abundance of high quality native forage and supplemental food resources occurring across the pine-dominated site. On our site hard mast producing hardwoods are not abundant, and are actively suppressed by prescribed fire and mechanical removal.

We used body mass as a measure of nutritional condition, and therefore cannot directly address impacts on fitness. While body mass has been linked to fecundity in numerous cervids [46]-[50] we acknowledge body mass may not influence productivity. However, our results demonstrate a behavioral process that can affect population-level processes. We found no support for a cohort effect on body mass of adult female white-tailed deer [51], [55]. Mech et al. [54] described cohort effects in white-tailed deer populations in Michigan, USA, resulting from environmental conditions that persist through generations. Strickland el al. [57] found white-tailed deer in Mississippi, USA, were able to overcome cohort effects presumably because they faced less extreme climatic conditions. Our results are similar to [57] and suggest deer on our site did not face climatic conditions or densities required to maintain cohort effects. We speculate that deer on our site are maintained at densities that are low relative to resource availability and are likely able to compensate for cohort effects by increasing annual resource intake.

Coyotes are capable of preying on large cervids [87] and are predators of adult [33], [88], and juvenile [27] white-tailed deer. However, most studies identifying coyotes as significant predators of adult white-tailed deer occurred in northern temperate climates where predators are aided by deep snow (For review see [27]). In the southeastern USA, coyotes prey on white-tailed deer fawns [34], but less evidence exists for adult predation [89]. The lack of evidence for coyote predation on adult white-tailed deer in the Southeast does not limit the potential for NCEs. Our results support the prediction that NCEs can occur when direct effects of predation are inconsequential [90], and demonstrate that the risk of predation and the burden of antipredator behavior may be inequitably distributed across populations or foraging groups [91], [92]. For example, adult female white-tailed deer are less susceptible to predation than fawns, but disproportionately assume the responsibility of antipredator behaviors within a foraging group or population. This inequitable distribution of risk and antipredator response suggests that motivation of antipredator behaviors is evolutionary fitness rather than individual survival.

There has recently been considerable interest in developing a theoretical framework that predicts the occurrence and strength of NCEs, using predator, prey, and environmental attributes [90, 93-95]. While evidence of predator-mediated behaviors is abundant, predicting when these behaviors have NCEs remains elusive. Predicting NCEs as a function of predator hunting mode has been supported using numerous invertebrate and vertebrate predators and consumers [93], [94]. This theory predicts wide-ranging active hunters, such as canids, would have weaker NCEs than would ambush hunters. Empirical evidence testing this theory in large terrestrial vertebrates has produced conflicting results. For example, the effects of grey wolves (*Canis lupus*) on elk (*Cervus elaphus*) antipredator behaviors in the Greater Yellowstone Ecosystem are well-documented [11], [12], [21]. However, the potential of these behavioral processes to result in NCEs remains controversial [60], [83], [84]. Our results suggest coyotes, a wide-ranging and active-hunting predator, with limited lethality to adult white-tailed deer induced antipredator behaviors that result in a measurable response at the population level. These results support the assertion of Creel [95] that prey attributes may improve prediction of the occurrence of NCEs. However, when considering model systems that include coyotes for the development of a theoretical framework predicting the occurrence of NCEs, it may be important to acknowledge coyote dietary plasticity and their ability to achieve high densities in the absence of larger predators, which may allow coyotes to exert an inflated ecological influence [44].

Considerable effort has been allocated to better understand the effects of coyotes in recently colonized portions of their range, particularly in terms of white-tailed deer interactions [96]. However the NCEs of these interactions have been largely unreported, and may be substantial. Coyotes may be responsible for restoring the ecology of fear to ecosystems without other predators in the eastern USA [26]. Predator-sensitive foraging may relieve herbivory pressure on plant communities and induce behaviorally mediated trophic cascades [4], [5], [82]. Coyotes can influence white-tailed deer site selection, body mass, and recruitment [34], [62]; demonstrating the potential for both density- and behaviorally mediated trophic cascades [4], [5], [97]. The recently colonized region of the coyotes' range contains many ecosystems that have been degraded by overabundant deer populations [36], [39]. If the results from our experiment generalize across these systems, there is great potential for behaviorally mediated food web dynamics and ecosystem processes. We suggest ignoring the NCEs in predator prey interactions can lead to a dramatic underestimation of predator impacts within food webs. Future studies should evaluate the effects between resource competition and predation risk on foraging decisions, and site selection when risk and resources are heterogeneous across the landscape.

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Table 2.1. Name, description, anticipated relationship, and represented hypothesis of variables used to predict harvest weights of adult (≥ 2.5 yrs) female white-tailed deer on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011.

Variable	Description	Anticipated Relationship	Hypothesis
Coyote Index	Coyote track count abundance index	-	Top-down
Lactation	Evidence of lactation at harvest	-	Individual
Julian Date	Modified Julian date of harvest, 1-93 (Oct 15- Jan15)	-	Individual
Age	Age class (2.5, 3.5, ≥4.5 years)	+	Individual
Rain	Total annual growing season precipitation (Mar-Sept)	+	Bottom-up
Deer Index	Deer track count abundance index	-	Bottom-up

Table 2.2. Models, number of variables (K), second-order Akaike's Information Criterion (AIC_c), distance from the lowest AIC_c (ΔAIC_c), and model weight (w_i) for models independent of coyote abundance index, used to predict live mass (kg) of 476 adult female white-tailed deer on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011 independent of predation risk. We present models with $\Delta AIC_c \geq 2$ in order of likelihood of being the best model.

Models	K	AICc	ΔAICc	*wi*
Age[a] + Lac[b]	7	2926.482	0.000	0.227
Age + Lac + JD[c]	8	2927.598	1.115	0.130
Age	6	2927.790	1.307	0.118
Age + Lac + Deer[d]	8	2928.110	1.627	0.101
Age + JD	7	2928.269	1.743	0.095
Age + Lac + Rain[e]	8	2928.26	1.786	0.092
Age + Lac + JD + Deer	9	2929.064	2.582	0.062
Age + Lac + JD +Rain	9	2929.291	2.809	0.055
Age + Rain +JD	8	2929.878	3.395	0.041
Age +Lac +Rain + Deer	9	2930.074	3.591	0.95

[a] Age estimated from tooth replacement and wear categorized as 2.5, 3.5, ≥4.5 years

[b] Evidence of lactation at harvest

[c] Modified Julian date of harvest, 1-93 (Oct 15=1; Jan15=93)

[d] Deer abundance index

[e] Total annual growing season precipitation (Mar-Sep)

Table 2.3. Comparison of the best model predicting body mass of adult female white-tailed deer with and without the coyote abundance index, number of variables (k), second-order Akaike's Information Criterion (AIC_c), distance from the lowest AIC_c (ΔAIC_c), and model weight (w_i) for models used to predict live mass (kg) of 476 adult female white-tailed deer on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011. We present models in order of likelihood of being the best model.

Models	K	AICc	ΔAIC_c	w_i
Age [a] + Lac [b] + Coyote [c]	8	2923.781	0.000	0.794
Age + Lac	7	2926.482	2.702	0.206

[a] Age estimated from tooth replacement and wear categorized as 2.5, 3.5, ≥4.5 years

[b] Evidence of lactation at harvest

[c] Coyote abundance index

Table 2.4. Parameter names, estimates, standard error, and 95% confidence intervals calculated for all parameters included in the best model used to predict live mass (kg) of 476 adult female white-tailed deer on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011.

Parameter	B	SE	L CI	U CI
Intercept	-0.524	0.566	-4.612	-0.944
Age 3.5	2.856	0.543	1.777	3.906
Age 4.5	2.895	0.676	1.558	4.205
Coyote Index	-1.224	0.552	-2.306	-0.246
Lactation	-1.021	0.529	-1.966	0.135

Table 2.5. ANOVA table for best linear mixed model predicting body mass of 476 adult, female white-tailed deer on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011. We used Satterthwaite approximation for degrees of freedom and set alpha =0.05.

Source of Variation	Df	Sum Sq	Mean Sq	F-value	Denom	P-Value
Age[a]	2	950.04	475.02	18.08	467.96	>0.001
Lactation[b]	1	86.05	86.05	3.71	470.47	0.054
Coyote[c]	1	127.94	127.94	4.91	13.35	0.045

[a] Age estimated from tooth replacement and wear categorized as 2.5, 3.5, ≥4.5 years

[b] Evidence of lactation at harvest

[c] Coyote abundance index

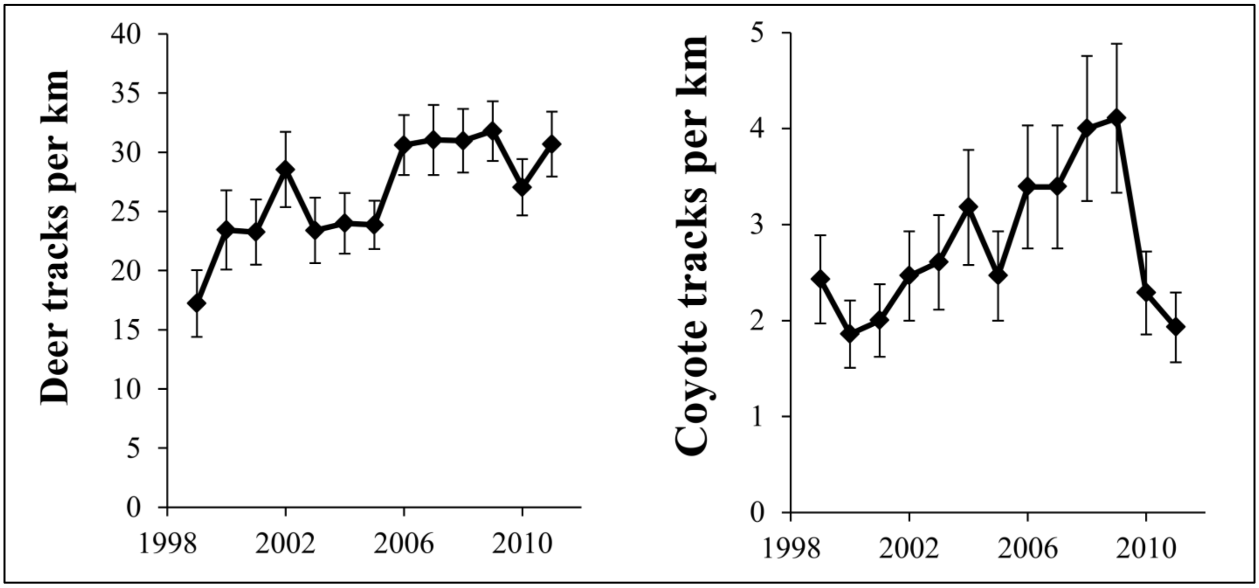

Figure 2.1. Mean annual white-tailed deer and coyote detections per km transect observed on 28 1-km Track Count transects distributed across the on the Joseph W. Jones Ecological Research Center, Georgia, USA, from 1999-2011. Error bars represent standard error.

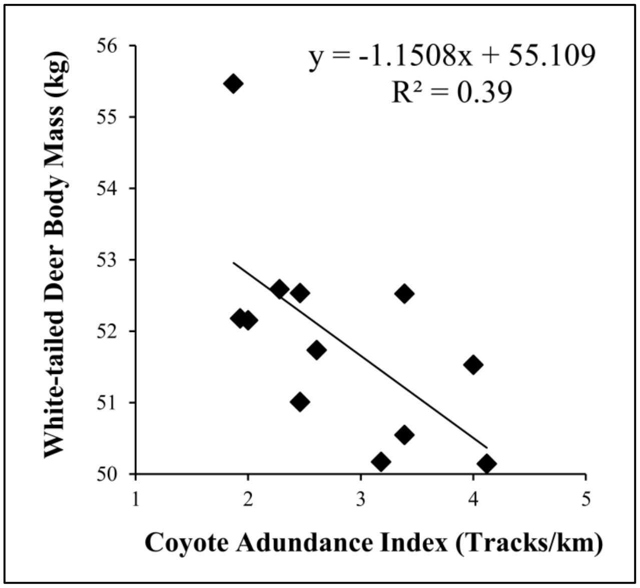

Figure 2.2. Correlation between annual mean body mass at harvest of adult (≥2.5 year) female white-tailed deer and annual coyote abundance index based on track count transects on the Joseph W. Jones Ecological Research Center, Georgia, USA, during 1999-2011. Displayed trend line, data points, linear regression model and R^2 value (t=-2.54, df=10, P=0.029).

CHAPTER 3

PREDATOR-SENSITIVE FORAGING IN A LONGLEAF PINE SAVANNA: EFFECTS OF PREY REFUGIA AND GROUP DYNAMICS ON WHITE-TAILED DEER VIGILANCE [2]

[1.] Cherry, M. J., L. M. Conner, and R. J. Warren. To be submitted to *Animal Behaviour*

ABSTRACT: Costs associated with antipredator behaviours can have profound effects on prey populations. We investigated seasonal and sex-specific effects of predation risk on white-tailed deer (*Odocoileus virginianus*) foraging behaviour by manipulating predator distributions through exclusion. In 2003, at the Jones Ecological Research Center, in Georgia, USA, we identified eight, approximately 40-ha plots, and randomly selected four to receive a predator exclusion treatment, while remaining plots served as controls. We examined the effects of predator exclusion and group conditions on the behavioural state (i.e., feeding or vigilant) of foraging white-tailed deer at baited camera traps. We determined the behavioural state of 25,828 white-tailed deer observations in predator exclosures and controls during spring, summer and winter of 2011-2012. We used generalized linear mixed models to test for differences in behavioural state of white-tailed deer foraging in predator exclosures and controls, while examining the effects of season, group size and composition of age-sex classes of white-tailed deer. The proportion of time spent feeding was highest in the spring followed by summer and winter. Males spent 7% more time feeding in predator exclosures than control plots during the winter when males were in post-rut conditions ($Z=2.23$, $P=0.017$). Females spent 5% more time feeding during the summer concurrent with fawning ($Z=4.5$, $P<0.001$). In general males were more vigilant than females and demonstrated a stronger response to predator exclusion. Our results demonstrate experimentally that predation risk influences behaviour of foraging prey, and that white-tailed deer alter their vigilance levels at a fine scale in response to predator distributions. Variation in foraging-vigilance tradeoffs may affect nutritional condition of white-tailed deer and the effects of their foraging on vegetation communities. We propose that the effects of predators on white-tailed deer in the southeastern USA transcend predation on neonates and juveniles, and influence foraging behaviour of the entire population. Ignoring predation risk effects will result in a dramatic underestimation of the influence of predators on prey populations.

KEY WORDS: *Canis latrans*, coyote, non-concumptive effects, *Odocoileus virginianus*, predation risk effects, predator exclosure, longleaf pine

INTRODUCTION

There is a growing appreciation for the importance of the predation risk effects of predators on prey populations, communities, and ecosystems (Werner and Peacor 2003, Schmitz et al. 2004, Peckarsky et al. 2008, MacLeod et al. 2014). Predators can affect prey vigilance (Hunter and Skinner 1998), habitat selection (Creel el al. 2005), diet selection (Edwards 1983), physiological stress (Clinchy et al. 2013), and fecundity (Zanette et al. 2011). These non-consumptive interactions can have profound effects on prey fitness and food web dynamics that are independent of direct mortality (Creel and Christianson 2008).

Time allocated to vigilance while foraging is a common measure of antipredator behaviour, perhaps because it can be directly related to resource acquisition rates, and then by extension to prey fitness and impacts on lower trophic levels (Lima and Dill 1990, Brown et al. 1999, Laundre et al. 2001, Childress and Lung 2003, Brown and Kotler 2004). Prey vigilance should vary through time and space to maximize resource acquisition and minimize the risk of predation (Lima and Dill 1990). The optimal antipredator response should equilibrate along a gradient of opposing risks of starvation (or loss of fitness) and predation (Brown 1999), and a behavioural response to one risk type often requires an increase in tolerance of the opposing risk. Prey species engage in predation risk-prone behaviours to acquire resources when nutritional condition is compromised, and under high predation risk conditions prey restrict foraging (Sih 1980, McNamara & Houston 1987). Brown et al. (1999) described these foraging tradeoffs as the ecology of fear, and suggest that the behavioural response to predation risk influences prey fitness and impacts on ecosystems. The effects of predation risk on trophic interactions, and prey nutritional condition and fecundity have been described in a wide range of taxa in numerous systems (Werner and Peacor 2003, Schmitz et al. 2004, Creel et al. 2007, Christianson and Creel 2010, Zanette et al. 2011).

In sexually dimorphic ungulates, the sexes experience different perceived predation risk and resource demands based on morphology, and therefore exploit resources differently, inducing sexual segregation (McCullough et al. 1989, Main et al. 1996, Bowyer et al. 2004). Females are predicted to experience greater risk of predation and have stronger antipredator responses, as described in pronghorn (*Antilocapra Americana*; Lipetz and Bekoff 1982) and elk (*Cervus elaphus*; Childress and Lung 2003; Winnie and Creel 2007). However, numerous ungulate species show opposite trends where males are more vigilant than females, including African buffalo (*Syncerus coffer*; Prins and Iason 1989), Burchell's zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus defassa*; Burger and Gochfeld 1994) and springbok (*Antidorcas marsupialis*) (Bednekoff and Ritter 1994, Burger et al. 2000); or no sex-specific trend at all, such as in kob (*Kobus kob*), and impala (*Aepyceros melampus*; Burger and Gochfeld 1994). Furthermore, Ginnett and Demment (1997) demonstrated that in giraffe (*Giraffa Camelopardalis*) males were more vigilant than females during the wet season while the opposite was true during the dry season. Across ungulate species there is considerable sex-specific variation in antipredator strategies for mitigating the risk of predation while acquiring and processing resources. Females and young are often more susceptible to predation than larger bodied males (McCullough et al. 1989, Main et al. 1996, Ruckstuhl & Neuhaus 2000, Bowyer et al. 2004), but males can experience a greater risk of predation, such as in wolf-elk systems (Huggard 1993, Mech et al. 2001) and cheetah-Thompson’s gazelles systems (*Acinonyx jubatus-Gazella thomsoni*; Fitzgibbon 1990).

Like other ungulates, white-tailed deer (*Odocoileus virginianus*) juveniles are less vigilant than adults; however, sex-specific variation in vigilance rates remains unclear (LaGory

1986, Lark and Slade 2008, Lashley et al. 2014). LaGory (1986) and Lark and Slade (2008) found no difference in vigilance levels between the sexes, but Lashley et al. (2014) observed greater vigilance in females and suggested this pattern could result in variation in feeding durations, daily movement, and group sizes resulting in sexual segregation as predicted by Ruckstuhl and Neuhaus (2000). It is important to note that of these studies only Lashley et al. (2014) used bait to congregate individuals for observation. The studies by Lashley et al. (2014) and Lark and Slade (2008) were conducted in systems where coyote (*Canis latrans*) and bobcat (*Lynx rufus*) were the primary non-human predators of deer, whereas in LaGory's (1986) study site bobcats were the only non-human predator of deer. It is unknown if the variation in vigilance observed in these studies was the result predation risk from current predator communities, anthropogenic risk, or remnant behaviours that were selected for during the evolution of the species.

White-tailed deer form loose aggregations where individuals freely join and leave a group (LaGory 1986). This social structure allows white-tailed deer to fluctuate group size relative to foraging conditions (Hirth 1977), presumably forming "optimal" group sizes that maximize foraging, while minimizing predation risk. Dominance behaviour is important in social ungulates when there is completion for resources, mates, or space (Taillon,& Côté 2006). Therefore the composition of groups can also have strong effects on foraging. Ozoga (1972) demonstrated that male white-tailed deer dominated females and juveniles and that the number of aggressive interactions increased as resource availability decreased. Predation risk can decrease functional resource availability by increasing the cost of resource extraction, thereby decreasing the net energy available from a resource (Brown et al. 1999). In other systems, predation risk can increase sexual segregation (Croft and Krause 2004).

White-tailed deer can have a profound influence on forested ecosystems and have existed in the absence of non-human predators across much of their range for decades (Côté et al. 2004). In the absence of predation, white-tailed deer often achieve densities incompatible with human interests and ecological processes (Warren 1997). Stromayer & Warren (1997) suggested white-tailed deer herbivory in the eastern USA can lead to alternative stable states that require drastic land management actions, beyond merely reducing white-tailed deer densities, to restore ecosystems to previous successional trajectories. Cromsigt et al. (2013) suggested that ungulate management should incorporate the ecology of fear (Brown et al. 1999) and manipulate the risk perceived by ungulates to reduce use of or modify behaviour in areas where herbivore impacts are not desired. The landscape of fear perceived by white-tailed deer has likely experienced considerable change during the last several decades as coyotes colonized many systems that lacked apex predators for nearly a century (Laundre et al. 2001, Gompper 2002). Coyotes evolved as a mesopredator with natural history traits, such as high productivity and the ability to achieve high abundances, which may allow coyotes to exert a powerful ecological influence on trophic interactions, when assuming the role of apex predator (Gompper 2002, Ripple et al 2013). Over the last few decades coyote populations have achieved abundances in eastern North America capable of influencing demography of white-tailed deer populations (Kilgo et al. 2010, 2012). This emerging predator-prey dynamic likely has profound effects on white-tailed deer foraging behaviour, yet those interactions remain poorly understood.

We examined seasonal effects of predator exclusion on adult male, adult female, and juvenile white-tailed deer antipredator behaviours. We hypothesized age-sex classes perceived predation risk on unique seasonal cycles and that predator exclusion treatment effects would vary temporally. Specifically, we predicted that predation risk would be greatest for adult female white-tailed deer during the summer, associated with fawning, and for adult males during the winter, associated with post-rut conditions (Ballard 2011). We hypothesized that predation risk would be greater for juvenile white-tailed deer during the summer than winter, but energetic demands of growth and inexperience would compromise antipredator responses. We predicted that vigilance would be inversely related to group size (Roberts 1996) and that foraging in mixed-sex groups would reduce adult male vigilance and increase adult female and juvenile white-tailed deer vigilance (Ozoga 1972). Adult male white-tailed deer, particularly subordinates, could benefit from reduced social conflict among males by foraging with female groups (Ruckstuhl 1998). Adult female and juvenile white-tailed deer may increase vigilance in mixed-sex groups due to male aggression and social conflict (Ozoga 1972, Taillon, & Côté, 2006). Further, we hypothesized presence of juveniles would cause one of two mutually exclusive outcomes for adult female foraging: (1) increased vigilance as an antipredator response, or (2) decreased vigilance because of increased energetic requirements during lactation.

In this study we investigated seasonal and sex-specific effects of predation risk on white-tailed deer foraging behaviour by manipulating predator distributions through exclusion. We experimentally isolated the effects of the predator community, by altering predator abundances independent of habitat cues, and anthropogenic risk. We investigated the effect of group dynamics on foraging behaviour under controlled conditions of spatial and temporal variation in levels of predation risk. We discuss the ecological implications of predator-sensitive foraging behavior in white-tailed deer.

METHODS AND MATERIALS

Study Site

Our research took place on Ichauway, the 12,000-ha outdoor research site of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia, USA. Ichauway included approximately 7,250 ha of longleaf pine (*Pinus palustrus*) stands. Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens–Nyssa biflora*) limesink ponds (Boring 2001). Approximately 10% (120 ha) of the site was comprised of cultivated wildlife openings and approximately 50% (6,000 ha) of the site was burned annually. White-tailed deer abundance was managed through adaptive harvest to maintain densities well below the nutritional carrying capacity to maximize herd health and minimize herd effects on the ecosystem. Estimated white-tailed deer densities were between 3.8-5.8 deer/km^2 during the study (B. T. Rutledge, unpublished data). Coyotes and bobcats were the only non-human predator of white-tailed deer on site (Howze et al. 2009, Nelson et al. in review).

Predator Exclusion

We chose eight, approximately 40 ha sites of similar habitat composition (i.e., longleaf pine-dominated canopy and native ground cover) to serve as study plots, of which four were randomly selected to serve as mesopredator exclosures and the remaining four were controls. At plots chosen for mesopredator exclusion, we constructed a woven-wire (10 x 20–cm mesh) fence with electric wire attached to E2000 electrical fence chargers (Twin Mountain Fence Company, San Angelo, TX) along the top, middle, and bottom to deter mesopredators from climbing or digging under fences. Predator exclosures were trapped using a combination of soft-catch (Woodstream Corp., Lititz,PA) and cage (Tomahawk Live Trap Company, Tomahawk,WI) traps. Trapping efforts targeted raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), grey foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), coyotes and bobcats. Captured predators were relocated just outside the exclosure. To ensure the effectiveness of the treatment, sites were trapped twice annually for the duration of the study. Prescribed fires were conducted on all plots biannually. Predator exclosures were permeable to deer and were smaller than deer home ranges reported in the literature (Stewart et al. 2011). Additional details on our predator exclosures and their effectiveness in excluding coyotes can be found in Conner et al. (2010) and Smith et al. (2013). Trapping of mesopredators was conducted under Georgia state wildlife collection permit 29-WJH-13-203.

Field Experiment

We used camera traps to measure the effects of predation risk on foraging white-tailed deer under various risk conditions (Altendorf et al. 2001, Hernández et al. 2005, Lashley et al. 2014). We tested the effects of predation risk on white-tailed deer foraging behaviour under three unique hypothesized conditions: (1) Spring - low risk for all, high resources, (2) Summer - high risk for females low risk for males, high resources, (3) Winter - low risk for females, high risk for males, low resources. We based these assumptions of risk and resources on predator diet analysis from Ichauway (Howze 2009), primary literature describing white-tailed deer predation (Ballard 2011), and our site-specific knowledge of the chronology of resource availability. In our investigation of the effects of predators on deer foraging behaviour, we experimentally isolated spatial variation in predation risk by predator exclusion and standardizing resource availability and habitat structure (i.e., quality of concealment cover) using three approaches: (1) the random assignment of the predator exclosure treatment to approximately 40-ha candidate plots of similar habitat composition; (2) selecting camera stations within plots with consideration for habitat attributes at multiple-scales (i.e., patch type, micro-site characteristics); and (3) the addition of a supplemental resource at the foraging stations.

We established two foraging stations within each predator exclosure and control plot (n=16) to conduct behavioural surveys. Foraging stations were placed in stands characterized by a longleaf pine canopy with 22-44m^2/ha basal area, a native groundcover, and ≥ 100 m from roadways or habitat edges. Prescribed fire was conducted in all study plots during February, 2011. We mounted a white-flash, remote-sensing camera (Cuddieback Capture Trail Camera, Non Typical, Inc. Green Bay, WI) with the latency time between photos set to 5 minutes, on the north face of a tree at each foraging station. We conducted 14-day surveys, spring (May) and summer (Aug-Sept) of 2011 and 2012, and winter (February) of 2012. Fall surveys were not conducted because baiting is prohibited during deer hunting season on site. White-tailed deer hunting occurred in all plots during both years from mid-October through mid-January, and likely had little effect on results because of extremely low hunter densities (1 hunter per 4,615 ha/day). Camera sites were baited with 18 liters of whole corn at the onset of each trial and every two days during trials.

Behavioral Interpretation and Photograph Analysis

We categorized the behavioural state of each white-tailed deer observation as actively feeding (i.e., head down, actively consuming bait) or not. We chose to model actively feeding behaviour as opposed to vigilance because it was a less subjective designation and the effects of vigilance on feeding was ultimately the consequence that most interested us in this experiment. We interpreted means developed from this variable as the proportion of time actively feeding while foraging at baited stations. We identified age of observed white-tailed deer as adult or juvenile based on morphology and pelage characteristics, and determined sex based on presence or absence of antlers. We assigned a group size to each observation by counting the white-tailed deer in the photograph and classified groups as mixed-sex groups if they contained ≥ 1 male and ≥1 female deer. We extracted time data from each image, and categorized the time into three classes based on survey-specific times for sunrise and sunset: (1) day - began 1.5 hours after sunrise and ended 1.5 hours before sunset; (2) crepuscular - 1.5 hours before and after legal sunrise and sunset; and (3) night - began 1.5 hours after sunset and ended 1.5 before sunrise.

Vigilance data analysis—We used photographic evidence to test the hypothesis that white-tailed deer are less vigilant in the absence of predators, while also investigating the effects of season and group dynamics. Similar to Lashley et al. (2014), we modeled behavioural state (i.e., foraging=1, and not foraging=0) as a binary response variable using generalized linear mixed models (GLMM) with a binominal error distribution and a logit link function (Bolker et al. 2009). To test for differences in time spent foraging between age-sex class effects, we used all deer detections that could be assigned to an age-sex class to model behavioural state as a function of independent variables including, class (adult male, adult female, or juvenile), group size, mixed-sex group (yes or no), predator exclusion treatment (yes or no), season (spring, summer, winter), and a predator exclosure treatment by season interaction. To quantify impacts of independent variables and their interactions, and to test age-sex class specific hypotheses, we developed separate models for adult male, adult female, and juvenile white-tailed deer. All age-sex class models predicting behavioural state contained predator exclusion treatment (yes or no), season, a predator exclosure treatment by season interaction, group size, and mixed-sex group (yes or no). The adult female white-tailed deer model also contained presence of juvenile (yes or no) as an independent variable. The juvenile white-tailed deer model was the same as the adult male model except the independent variable “season” contained only two classes (i.e., summer and winter), because we could not distinguish juveniles from adults during spring surveys. We set plot (eight classes, i.e., predator exclosure or control plots), survey (five classes), and time of day (three classes; i.e., day, crepuscular, and night) as random effects in all models. We used Wald’s statistic for inference and set alpha=0.05.

RESULTS

Vigilance While Foraging

We had 25,828 detections of white-tailed deer and used those data to estimate factors influencing foraging behaviour. We observed 15,175 and 10,653 deer detections in predator exclosures and controls, respectively. We observed 5,121 adult male white-tailed deer (i. e., visibly antlered deer), 16,445 adult (i.e., ≥1.5 years of age) female white-tailed deer, and 1, 553 juvenile (i.e., ≤1.5 years of age) white-tailed deer. We also detected 2,709 white-tailed deer (10% of observations) that we could not accurately categorize in an age-sex category, and therefore, did not include in analysis, but these observations were included when estimating group size.

Male white-tailed deer spent less time feeding than females (Z=2.82, P=0.004) or juveniles (Z=8.12, P<0.001). The proportion of time male white-tailed deer spent feeding did not vary by season or predator exclosure treatment independently, but was greater (Z=2.23, P=0.027, Table 1) in predator exclosures (mean ± se; 0.28 ± 0.03) than in control plots (0.21 ± 0.01) during winter. The proportion of time male white-tailed deer spent feeding was 6% greater in mixed-sexed groups than male groups (Z=2.3, P=0.021). Group size had no effect on male time spent feeding.

The proportion of time female white-tailed deer were feeding differed significantly by season (spring [Z=referent]), < summer [Z=-4.02, P< 0.001] < winter [Z=3.07, P=0.002], Figure 1). The proportion of time spent feeding was greater (Z=4.23, P<0.001) in predator exclosures (0.30 ± 0.001) than control plots (0.25 ± 0.001) during the summer, but not during other seasons. In contrast to males, mixed-sex groups had no effect on female foraging, but time spent feeding increased with group size (Z=2.90, P=0.004, Figure 2). The presence of juveniles increased the time female deer spent feeding (Z=2.06, P=0.040). The proportion of time juvenile white-tailed deer spent foraging followed the same trends, but did not differ significantly by predator exclosure treatment, season, or the interaction. Foraging in mixed-sex groups decreased the proportion of time juvenile white-tailed deer spent feeding by 33% in control plots, and 10% in predator exclosure plots (Z=-3.83, P<0.001; Figure 2). Group size had no effect on time spent foraging (Figure 3).

DISCUSSION

Our results demonstrate that predation risk can influence white-tailed deer foraging behaviour. Predator-sensitive foraging has been used to explain observations in natural systems, but experimental evidence using large terrestrial vertebrates under free-ranging conditions is rare due to scales required for investigation (Childress and Lung 2003). We demonstrated white-tailed deer foraging behaviour is influenced by spatial and temporal variation in predation risk and that group dynamics have strong effects on foraging. These results suggest that white-tailed deer foraging behaviour is in accordance to a landscape of fear (Laundre et al. 2001) such that landscape topography, which connotes variation in perceive predation risk, may predict spatial variation in deer herd condition or herbivory impacts. Our results suggest the effects of predators on white-tailed deer in the southeastern USA likely transcend juvenile predation and may influence foraging behaviour of the entire population.

The predation risk hypothesis for sexual segregation (Ruckstuhl & Neuhaus 2000; also referred to as the reproductive strategy hypothesis by Main et al. 1996) predicts that larger bodied males are less susceptible to predation than females or juveniles, and therefore can exploit riskier resources. However, in this study males were more vigilant than females and displayed stronger predator exclusion treatment effects. We suggest two explanations for these results. First, male white-tailed deer may experience much greater risk of predation than was expected. Coyotes are capable of preying on large cervids including moose (*Alces alces*; Benson & Patterson 2013) and are known predators of adult white-tailed deer (Whitlaw et al. 1998, Patterson et al. 2002). Lingle and Pellis (2002) reported coyotes preferentially preyed upon larger mule deer (*Odocoileus hemionus*) over sympatric white-tailed deer. In other systems, large male ungulates are disproportionally preyed upon by predators (Fitzgibbon 1990, Huggard 1993, Mech et al. 2001). Perhaps a similar dynamic is at play in our study system, where counter to the predation risk hypothesis, larger-bodied males are at greater risk of predation. However, in the southeastern USA, coyotes can prey heavily on white-tailed deer fawns (Kilgo et al. 2012), and some evidence exists for adult female predation (Chitwood et al. *in press*), but we are unaware of any studies describing coyotes as a relevant mortality source for adult male white-tailed deer in this region. Most studies identifying coyotes as significant predators of adult white-tailed deer occurred in northern temperate climates where predators are aided during winter by deep snow, and reduced body condition of white-tailed deer (Ballard 2011).

An alternative, and we believe more likely, explanation for adult males showing greater predator effects than females, is that the risk of direct predation experienced by an age-sex class does not directly predict the strength of the predation risk effect on that age-sex class in this system. The risk of predation is the probability of being consumed by a predator, while predation risk effects are a function of perceived risk, fitness, and the effectiveness and costs of antipredator responses (Brown et al. 1999). Antipredator responses and the associated costs to prey fitness and trophic interactions can occur when direct predation is inconsequential (Creel and Christianson 2008). Species that are not particularly effective at evading predators or cannot afford the foraging costs of antipiredator defenses, are predicted to experience high direct predation, but invest little in antipredator behaviors, and therefore have low predation risk effects. Alternatively, predation risk effects may be greater in species with little direct predation because those species have effective, but costly means to mitigate predation (Creel and Christianson 2008).

In our study system, juvenile white-tailed deer undoubtedly face the highest risk of predation. Yet, vigilance by juvenile deer was lower than for adult male and female white-tailed deer, likely because of energetic requirements for growth. These results suggest juveniles have high potential for numeric effects (direct predation), and lower potential for predation risk effects. We assumed adult male white-tailed deer experience the lowest risk of predation of all age-sex classes, due to the lack of published data describing adult male white-tailed deer predation in the southeastern, USA. Yet, male white-tailed deer displayed the greatest increase in time spent feeding while in the predator exclosures and the highest vigilance in the study, suggesting males have low potential for numeric predator effects through direct predation, but high potential for predation risk effects. Similar to juvenile white-tailed deer in our system, bull elk were disproportionately preyed upon by wolves during the winter compared to cows, and faced a higher risk of predation (Huggard 1993, Mech et al. 2001). However, in decreased body condition during the winter, bulls could not afford the foraging costs of antipredator behaviours and, therefore, suffered disproportionate direct predation, but likely lower predation risk effects (Winnie and Creel 2007). Cow elk faced lower risk of predation than bulls, but mounted a stronger antipredator response to the presence of wolves, and were more likely to experience predation risk effects (Creel et al 2007, Winnie and Creel 2007, Creel and Christianson 2008).

During the month following parturition, female ungulates face the greatest energetic demands of reproduction (Oftedal 1985) and the greatest risk of predation to their offspring (Barber-Meyer et al. 2008, Kilgo et al. 2012). In bison (*Bison bison*; Komers et al. 1993), domestic sheep (*Ovis aries*; Penning et al. 1995), and cattle (*Bos taurus*; Gibb et al., 1999) increased nutritional demands of lactation resulted in increased foraging. However, the presence of young resulted in increased vigilance in pronghorn (Lipetz and Bekoff 1982), roe deer (*Capreolus capreolus*; Linnel 1994), impala, wildebeest (Hunter & Skinner 1998), French Alpine ibex (*Capra ibex ibex*; Toïgo 1999), and elk (Winnie & Creel 2007), but had no effect on foraging in muskoxen (*Ovibos moschatus*; Oakes et al. 1992) and Rocky Mountain bighorn sheep (*Ovis Canadensis*; Ruckstuhl et al. 2003). In this study, the predator exclosure treatment effect on adult female white-tailed deer increased during the pulse of predation risk associated with the fawning season, but in contrast to Lashley et al. (2014), the presence of juveniles resulted in increased feeding. The discrepancy in our results and the findings of Lashley et al. (2014) may reflect fine-scale temporal variation in resource-safety foraging tradeoffs associated with reproductive chronology.

To increase fitness throughout reproduction, female deer balance safety-resource tradeoffs through adaptive allocation of effort to protection of neonates through increased vigilance, and investment in personal nutritional condition through increased foraging; We suggest immediately following parturition female deer likely increase foraging to meet energetic requirements of lactation, and at some point vigilance for protection of neonates is more important than foraging, and during gestation female deer should maximize their own nutritional condition. In this study, summer surveys were conducted during the first month post-partum when energy requirements for female ungulates increase 65-215% (Oftedal 1985, Robbins 1993,Parker et al. 2009). Winter surveys were conducted when juveniles were approximately seven months old and adult females were pregnant, when inadequate nutritional condition can reduce ungulate birth weights, neonate growth, and recruitment (Verme 1965, 1969; Hight 1967; Robinson & Forbes 1968; Thorne et al. 1976). In contrast, Lashley et al. (2014) surveyed white-tailed deer when juveniles were approximately 2.5 months of age (personal communication; M. Lashley) when energetic demands of lactation are decreasing and surviving juveniles are nearing recruitment and represent a substantial investment. Perhaps during our summer surveys energetic requirements for lactation were greater than predation risk, while in Lashley et al. (2014) demand for neonate protection through vigilance was greater than energetic requirements, and during our winter surveys females were investing in nutritional condition to meet the demands of gestation over protection of previous offspring. Variation in the effect of the presence of juveniles on female vigilance observed here and in Lashley et al. (2014) could also simply be explained by site-specific differences in predation risk or resource availability. Future work should investigate seasonal variation in vigilance behavior associated with pulses of risk and group dynamics at a fine temporal scale to better understand the foraging-safety tradeoffs associated with reproduction.

Male white-tailed deer increased time spent feeding while juvenile deer greatly decreased time spent feeding in mixed-sex groups, and counter to our predictions, female white-tailed deer foraging was not influenced by mixed-sex groups. These results suggest males can escape social conflict with other males and reduce vigilance by foraging with female groups. Similarly, sub-adult male bighorn sheep foraged in nursery and bachelor groups and altered behavior according to group type (Ruckstuhl 1998). However, when male deer forage in female-juvenile groups, juvenile foraging is reduced, presumably because of a male dominance behavior and social conflict (Ozoga 1972, Taillon, & Côté 2006). This process demonstrates that age structure of deer populations may have important indirect effects on fitness. For example if sub-adult males are over represented in the population, then sexual segregation likely decreases and consequently juvenile deer spend less time foraging, which could influence time to first reproduction or winter survival (Verme 1965, 1969).

Predator exclusion influenced the strength of the effect of group composition on foraging behavior of all age-sex classes. For example, during summer female white-tailed deer with juveniles spent 10% more time foraging than females without juveniles in control plots, but only 5% more time foraging in predator exclosures. These results suggest the energetic demands of fawn rearing are greater in the presence of predators. When male deer were present, juvenile deer decreased time spent feeding 33% in control plots, but only 10% in predator exclosure plots relative to when male deer were absent. These results suggest that male dominance behaviour is greater incontrol plots, perhaps because the cost associated with obtaining resources was greater under risky conditions (Brown et al. 1999). Male white-tailed deer increased time feeding in control plots from 17% to 27% by foraging in mixed-sex groups as opposed to male groups, but in predator exclosures, time spent feeding only increased from 27% to 29%. Interestingly, male white-tailed deer foraging in a male group in a control plot could equate to a virtually identical increase in time spent feeding by foraging in a mixed-sex group in the control plot or in a male group in the predator exclosure. We speculate that predation risk heightens social conflict by increasing the cost of acquiring resources, thereby decreasing the net profitability of available resources (Ozoga 1972, Lima and Dill1990, Brown et al. 1999, Brown and Kotler 2004).

In conclusion, predation risk is an important environmental factor that should be considered in the management of ungulates and other wildlife species (Cromsigt 2013). We provide empirical evidence that white-tailed deer modify antipredator behaviour according to spatial and temporal variation in predation risk. We demonstrate that even in systems without large apex predators, predation risk can still profoundly influence foraging behaviour of white-tailed deer and may be an important driver for ecological processes such as sexual segregation and herbivore-plant interactions. Future work should examine how these results extrapolate beyond our experimental treatments to landscapes where risk is a continuous variable and resources and risk are spatially and temporally dynamic.

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Table 3.1. Parameters estimates for logistic regression models predicting the behavioral state (i.e., actively feeding or vigilant) from digital images (n=25,828) of adult male adult female and juvenile white-tailed deer foraging at baited stations within predator exclosure and control plots during spring, summer and winter of 2011-2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Standard errors (SE), Odds ratio, z values, and probabilities a coefficient differs from 0 are also presented.

	β	SE	Exp(β)	z value	Pr(>|z|)
Adult male					
Intercept	-1.320	0.238	0.267	-5.544	<0.001
Predator exclusion	0.122	0.228	1.130	0.535	0.593
Summer	-0.363	0.235	0.696	-1.546	0.122
Winter	-0.442	0.261	0.643	-1.695	0.090
Mixed-sex group	0.196	0.085	1.216	2.306	0.021
Group size	-0.013	0.024	0.987	-0.545	0.586
Predator exclusion: Summer	0.169	0.173	1.184	0.976	0.329
Predator exclusion: Winter	0.488	0.220	1.628	2.215	0.027
Adult female					
Intercept	-0.842	0.164	0.431	-5.147	<0.001
Predator exclusion	-0.016	0.189	0.985	-0.082	0.935
Summer	-0.562	0.140	0.570	-4.019	<0.001
Winter	-0.549	0.179	0.577	-3.070	0.002
Presence of juvenile	0.130	0.063	1.139	2.056	0.040
Mixed-sex group	0.057	0.049	1.058	1.159	0.246
Group size	0.028	0.010	1.028	2.895	0.004
Predator exclusion: Summer	0.334	0.079	1.397	4.225	<0.001
Predator exclusion: Winter	-0.132	0.129	0.877	-1.017	0.309
Juvenile					
Intercept	-1.061	0.369	0.346	-2.876	<0.001
Predator exclusion	0.272	0.175	1.313	1.557	0.119
Winter	0.048	0.669	1.050	0.072	0.942
Mixed-sex group	-0.592	0.154	0.553	-3.832	<0.001
Group size	0.021	0.031	1.022	0.699	0.484
Predator exclusion: Winter	0.365	0.422	1.440	0.864	0.388

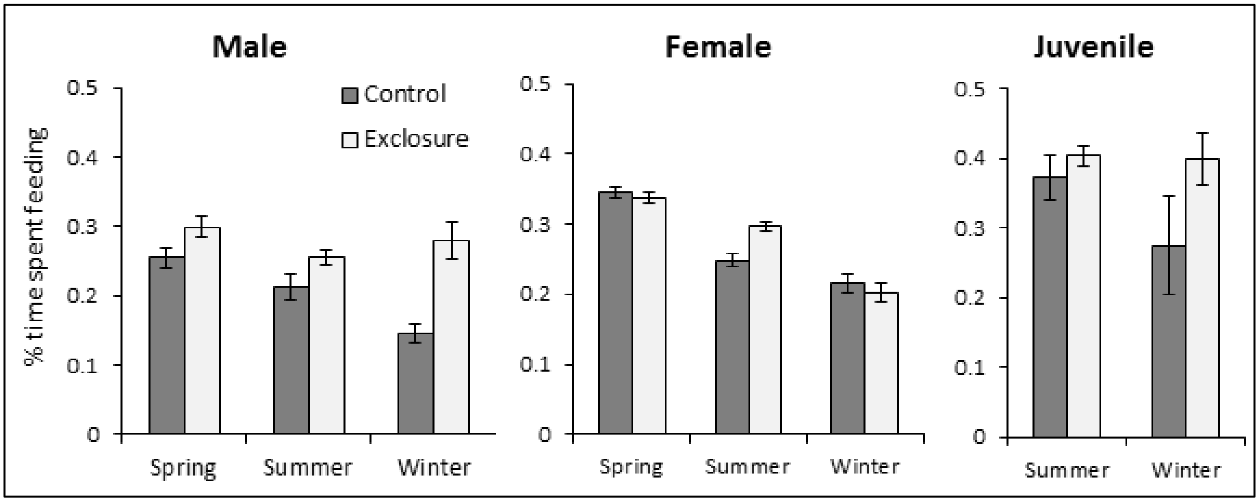

Figure 3.1. Percentage of time spent feeding by adult male, adult female and juvenile deer while foraging at baited camera stations (n=25,828 digital images) within predator exclosure and control plots during spring, summer and winter of 2011-2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Error bars represent standard error.

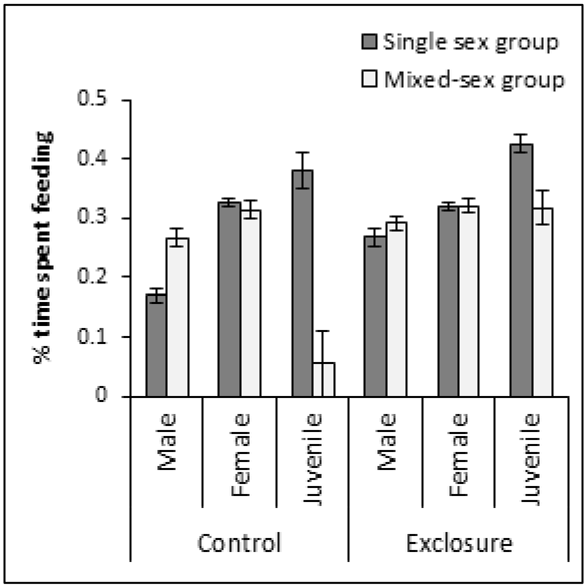

Figure 3.2. Percentage of time spent feeding by adult male, adult female and juvenile deer while foraging at baited camera stations (n=25,828 digital images) while in single-sex or mixed-sex groups within predator exclosure and control plots during spring, summer and winter of 2011-2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Error bars represent standard error.

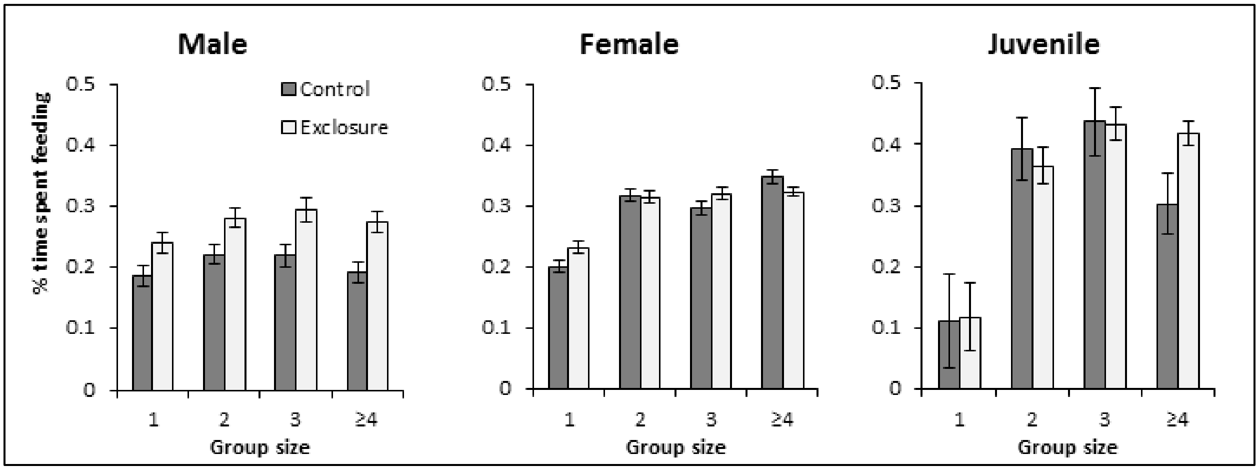

Figure 3.3. Percent of time spent feeding by adult male, adult female and juvenile deer while foraging at baited camera stations (n=25,828 digital images) while in various group sizes within predator exclosure and control plots during spring, summer and winter of 2011-2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Error bars represent standard error.

CHAPTER 4

COYOTE PREDATION RISK DECREASES WHITE-TAILED DEER OVULATION AND REPRODUCTIVE SUCCESS[3]

[1.] Cherry, M. J., K. E. Morgan, B. T. Rutledge, L. M. Conner, and R. J. Warren. To be submitted to *Ecology*

ABSTRACT: Predators can have powerful non-consumptive effects on their prey by inducing behavioral, physiological, and morphological responses. These non-consumptive effects may influence prey demography if they decrease birth rates or increase susceptibility to other sources of morality. Coyote (*Canis latrans)* range expansion in the USA has exposed eastern white-tailed deer (*Odocoileus virginianus*; hereafter deer) populations to increased predation risk. To evaluate effects of temporal variation in predation risk (i.e., coyote-deer ratios) on fecundity and reproductive success of deer, we examined ovaries for evidence of ovulation from deer harvested before and after a natural decline in coyote abundance occurring between 2005 (high coyote-deer ratio) and 2012 (low coyote-deer ratio) on the Joseph W. Jones Ecological Research Center in southwestern Georgia, USA. To investigate the effects of direct predation and fecundity on recruitment we also measured evidence of lactation at harvest, survival of marked fawns, and hunter-observed fawn-adult female (FAF) ratios harvested. We found that the proportion of females with evidence of ovulation ($Z=-2.13$, $P= 0.03$) and lactation ($Z=-2.34$, $P=0.02$) at harvest decreased with increasing predation risk. Survival of radio-tagged fawns to age at recruitment did not differ ($Z=0.031$, $P= 0.98$) between periods of high and low predation risk. Hunter-observed FAF ratios differed between periods of high and low predation risk ($X^2 = 4.124$, $df = 1$, $P=0.042$), increasing from 0.5 to 0.8 fawns per adult female. Calculated FAF ratios estimated using fecundity and survival data followed a similar trend, increasing from 0.4 to 0.6 fawns-adult female deer. Our results suggest coyotes can influence deer recruitment, independent of direct predation, through interactions that result in reduced fecundity. The physiologically mediated pathways, by which deer alter their reproductive strategy in response to environmental factors, may also be sensitive to other stressors such as predation risk. Our study demonstrates that coyotes can have strong non-consumptive effects on deer populations, and ignoring these effects may result in dramatic underestimation of impacts of expanding coyote populations on

ecosystems.

KEY WORDS: *Canis latrans*, Corpus lutea, fecundity, indirect effects, *Odocoileus virginianus*, non-consumptive effects, predation risk effects, recruitment, white-tailed deer

INTRODUCTION

Predators can have powerful non-consumptive effects on their prey by inducing behavioral (Hunter and Skinner 1998, Creel et al. 2005, Winnie and Creel 2007), physiological (Lima 1998, Clinchy et al. 2004; 2013, Travers et al. 2010), and morphological (Tollrian and Harvell 1999, Banks et al. 1999, Vamosi and Schluter 2004) responses. These non-consumptive effects may influence prey demography if they decrease birthrates or increase susceptibility to other morality factors (Creel and Christianson 2008). Changes in birthrates provide the most direct evidence of predation risk effects on prey demography as they are completely independent of direct killing. Non-consumptive effects can be greater than consumptive effects on prey demography (Preisser et al. 2005), but have seldom been evaluated in free-ranging vertebrate populations.

Literally hundreds of papers have demonstrated antipredator responses in prey, often at the cost of foraging (for review see Lima and Dill 1990, and Werner and Peacor 2004). Predator effects on prey fecundity can be substantial in aquatic and invertebrate systems (Preisser et al. 2005) and in free-ranging vertebrate populations (Creel et al. 2007, 2009, 2011; Travers et al. 2010; Zanette et al. 2011). Olaf and Halle (2004) experimentally applied a predator odor treatment to free-ranging grey-side vole (*Clethrionomys rufocanus*) populations and documented a decrease in the proportion of reproductively active females and recruitment of juveniles relative to control populations. Sheriff et al. (2009) presented pregnant wild-caught snowshoe hare (*Lepus americanus*) with a nonlethal “predator” (i.e., a trained dog) and documented reduced litter size and birth weights compared to a control group Zanette et al. (2011) exposed song sparrows (*Melospiza melodia*) to auditory predation risk cue and documented a 40% reduction in the number of offspring produced as a result of decreases in clutch sizes, egg hatchability, and nestling survival. The restoration of gray wolves (*Canis lupus*) in Yellowstone National Park, USA, caused elk (*Cervus elaphus*) to alter their vigilance (Laundre´et al. 2001, Winnie and Creel 2007), habitat selection (Creel et al. 2005), diet selection (Christianson and Creel 2008), and nutrient balance (Christianson and Creel 2010). These predator-induced behavioral changes were associated with reduced pregnancy rates and provided correlative evidence for predator-reduced prey fecundity (Creel et al. 2007). Creel et al. (2011) subsequently documented predation risk was inversely related to pregnancy rates in 10 independent elk populations. Evidence of predator effects on prey traits is abundant, and risk effects have been shown to influence reproduction and population demography in a diverse group of species, yet a framework for predicting the strength and occurrence of risk effects at the population, community, or ecosystem levels is just emerging (Preisser et al. 2007, Creel and Christianson 2008, Heithaus et al. 2009, Creel 2012).

The decline of apex predators (e.g., red wolf, *Canis rufus*) in the eastern USA during the 1800's may have led to a reduction of perceived predation risk for their main prey, the white-tailed deer (*Odocoileus virginianus*, hereafter deer). Since the mid-1900's, the extirpation of wolves was followed by a range expansion of coyotes (*Canis latrans*), and they now seem to occupy the ecological niche vacated by the wolf (Gompper 2002). Recent research demonstrates coyote predation on deer in the southeastern USA may reduce fawn recruitment and population growth rates (Howze et al. 2009; Kilgo et al. 2010, 2012), yet the non-consumptive effects of this evolving predator-prey dynamic have not been described.

As an iteroparous capital breeder, deer must balance the energetic costs of reproduction with body growth and maintenance to ensure future productivity. If nutritional costs of previous reproductive efforts are not recouped before the next breeding season, then capitol breeders may forgo reproduction (i.e., reproductive pause; Cameron 1994) or reduce maternal investment (Therrian et al. 2007, 2008; Taillon et al. 2013). In deer, fecundity is sensitive to nutritional condition, which can be influenced by population density and environmental factors (Rhodes et al. 1985, Mech 1987, Simard et al. 2014). However, ovulation itself is not an energetically demanding process, which suggests that decreased nutritional condition likely reduces fecundity through physiological processes that decrease or delay reproductive investment (Bronson and Manning 1991). Litter size in healthy deer populations average 1.6-1.8 fawns per adult female and increase with dam age (Rhodes et al. 1985, Ditchkoff 2011). Young deer must balance energetic demands for reproduction and growth and, therefore, body mass and condition in young cohorts are more susceptible to environmental factors than older, more resilient age cohorts (Gaillard et al. 2000, Strickland et al. 2008). Body mass and condition have been linked to fecundity in deer (Verme 1967, Strickland et al. 2008), but causative inference is difficult from these data alone because body mass and reproduction influence each other (Festa-Bianchet et al. 1998, Strickland et al. 2008, Simard et al. 2014).

In this study, we investigated the effects that temporal variation in coyote abundance had on deer fecundity by exploiting a natural decline in the coyote population. We tested whether perceived predation risk could affect fecundity by examining deer ovaries for evidence of ovulation (presence of ≥1 corpus luteum [CL]) before and after the coyote decline (Mansell 1971). To differentiate the effects of predation risk vs. direct predation on fecundity and recruitment, we measured multiple additional aspects of deer reproduction. We measured the proportion of female deer with evidence of lactation at harvest as a measure of fecundity and early survival. We evaluated survival to age of recruitment of radio-tagged fawns as a measure of direct predation. To measure recruitment, we calculated fawn-adult female ratios using hunter observation data, and corroborated those ratios by estimating fawn-adult female deer ratios using fecundity and survival data. We used these multiple measures of deer reproduction to evaluate relative contributions of the consumptive and non-consumptive effects of coyotes during periods of high and low predation risk.

METHODS AND MATERIALS

Study Site

We worked at the Joseph W. Jones Ecological Research Center (JC) in Baker County, Georgia which is an 11,736-ha, privately owned research center in the Upper Gulf Coastal Plain. The site consists primarily of *Pinus palustris–Aristida beyrichiana* (longleaf pine–wiregrass) savannas maintained with biannual prescribed fire. Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens–Nyssa biflora*) limesink ponds (Boring 2001). Approximately 10% of the property consists of cultivated wildlife openings. Grain is spread over approximately 60% of the site along feeding trails for bobwhite quail (*Colinus virginianus*) from February through May, but non-target species, including deer, also use this food source (Morris et al. 2010).

The JC's deer herd has remained at relatively low and stable densities of 3.8–5.8 deer/km^2 with approximately even sex ratios since the early 1990s (Rutledge 2013). Regulated hunter harvest has been applied annually to maintain low deer densities with the goal of maximizing herd health and minimizing negative ecological impacts on the ecosystem. Deer forage was abundant across the study area due to low deer densities and management practices including prescribed fire, maintenance of an open canopy, cultivation of forest openings, and broadcast of supplemental feed. The mean annual proportion of yearlings with evidence of lactation at harvest from 1997-2010 was 0.31± 0.03 (mean ± SE, n=289). Evidence of fawns successfully reproducing is indicative of excellent herd condition (Verme 1967). Therefore, we suggest that observed deer densities during this study never approached carrying capacity, at which density-dependent reductions in reproductive success might have occurred (Caughley 1976, Keyser et al. 2005). The site-wide recruitment rate averaged 0.5 fawns per adult female deer during 2007–2008 (Howze et al. 2009). Coyotes and bobcats (*Lynx rufus*) preyed on deer on our site, but food habits analysis and cause-specific fawn mortality data indicated that bobcats used deer considerably less than coyotes (Nelson et al. *in review*). For example, during the fawning season 43% of 173 coyote scats examined contained deer remains, whereas only 16% of 75 bobcat scats contained deer remains. Similarly, of 47 fawns monitored from 2007-2013, we documented 21 mortality events, and assigned 11 predation events to coyotes and only 2 to bobcats. (Nelson et al. *in review*).

Temporal Variation in Predation Risk: A Natural Experiment

Similar to Creel et al. (2007), we assumed predation risk was related to predator-prey ratios and used data collected annually on track count transects to develop coyote-deer ratios (Rutledge 2013). We performed track counts following Daniel and Freis (1971) using 28, 1-km long, systematically placed transects on roadways distributed across our study site. On our site, sandy roads provide an excellent tracking surface for detecting occurrence of wildlife. Roads were prepared for surveys using one pass with a road grader and two passes with a road rake pulled behind a tractor. Track count transects were monitored for three consecutive days during July and August annually during our study (i.e., 2005-2012). Between daily observations, transects were cleared of all tracks using a chain drag implement pulled behind an all-terrain vehicle. All detections in all years were made by the same observer. We developed annual coyote-deer ratios by calculating the mean number of detections for coyotes and deer per transect during a 3-day survey. We created an index of coyotes per 100 deer by dividing the mean number of coyote detections by the mean number of deer detections multiplied by 100 (Figure 1). For unknown reasons, the coyote population declined rapidly from 2009-2010,, , resulting in an approximately 50% reduction in coyote-deer ratios between our two study periods. Before the coyote decline (i.e., 2005-2008), the coyote-deer ratio ranged from 10.3-12.9 coyotes per 100 deer, compared to only 6.0-6.3 coyotes per 100 deer after the decline (i.e., 2011-2012). We used this variation in predator and prey abundances to establish a natural experiment investigating the effects of predation risk and direct predation on deer reproductive success and recruitment. We investigated the effect of coyote-deer ratios on the proportion of female deer with evidence of ovulation and lactation at harvest. Then, to investigate the relative effects of fecundity and survival on reproduction, we designated the two study periods as experimental groups—high predation risk (2005-2008) and low predation risk (2011-2013). This experimental design allowed us to integrate multiple data sources representing aspects of deer reproductive success that were collected during similar predation risk conditions (i.e., within our assigned high and low predation risk periods), but not necessarily during the same years, which allowed us to make inferences about the relative contribution of direct and indirect predator effects on recruitment.

Reproduction Data Collection

We collected samples from harvested deer during three hunting seasons: (1) 22 October 2005 – 15 January 2006, (2) 22 October 2006 – 15 January 2007, and (3) 22 October 2012 – 15 January 2013. During most of these hunting seasons, the same individual hunters were assigned to specific hunting blocks or areas throughout the JC; therefore, we suggest that there was no bias associated with harvest selection by hunters among all hunting seasons. Each deer was brought to a check station where we recorded harvest data (i.e., date, sex, age estimated by tooth eruption and wear [Severinghaus 1949], evidence of lactation, body mass, and tail-fat deposition). We estimated nutritional condition of harvested deer using body mass and an index of tail-fat deposition (Stockle et al.1978, Cook et al. 2001). We measured body mass (i.e., carcass weight before evisceration) to the nearest pound and converted to kilograms for analysis. Experienced personal measured tail fat deposition by palpation of the subcutaneous fat deposited at the base of the tail, and scored the amount of fat deposited on a 1-5 scale, with 1 being poor and 5 excellent condition.

To examine fecundity, we removed ovaries from a subset of the hunter-harvested female deer ≥ 1.5 years of age. Previous monitoring work by on-site deer herd managers determined the first estrous period consistently began by the beginning of December of each year; therefore, we standardized our analysis by using all samples collected during 1 December – 15 January of each year. This subset represented those females harvested during the latter portion of the hunting season each year, when CLs would be easily discernable on their ovaries (i.e., they had already ovulated and conceived during the current breeding season). We preserved ovaries collected during 2005-2007 in formalin; since then, JC discontinued use of formalin as a storage means, so we preserved ovaries collected during 2012-2013 in 90% ethanol. Ovarian bodies were easily discernible, regardless of method of preservation. Ovaries were sectioned sagittally with a scalpel into 3-4 slices and examined macroscopically and microscopically (4-20x) to count the number of CLs (Golley 1957, Langvatn 1992). We examined both ovaries from each deer to determine if the deer had ovulated and counted the total number of CLs. Paired ovary CL counts are directly related to *in utero* production rates (Mansell 1971).

We measured recruitment using three methods: (1) percentage of female deer with evidence of lactation at harvest, (2) survival of fawns marked shortly after birth that survived to age at recruitment), and (3) hunter-observed fawn-adult female (FAF) ratios. The percentage of harvested females with evidence of lactation (i.e., number of lactating deer harvested divided by total number of harvested female deer ≥2.5 years of age) is a measure of fecundity and early survival of fawns, but is a coarse measure of recruitment because it is a binary outcome that is not sensitive to litter size. Survival of marked individuals (i.e., number of radio-tagged fawns that survived ≥3 months divided by total number of collared fawns) measured the direct effects of fawn predation and other mortality sources on recruitment. Hunter-observed FAF ratios; total number of fawns observed divided by total number of adult female deer observed) were calculated from observations made by the same 14 hunter during all years. On our site these hunter observation data provide similar estimates of fawn-adult female ratios, following the Jacobson et al. (1997) technique using baited camera surveys (Howze et al. 2009). Each method measures an aspect of recruitment, but we consider hunter-observed FAF ratios the most direct measure of population-level recruitment, as it incorporates direct survival and fecundity.

We captured fawns to measure survival to age of recruitment by active searching with thermal infrared cameras, opportunistic fawn sightings, and by implanting adult female deer with photo-sensing vaginal implant transmitter (VITs; Advanced Telemetry Systems; Isanti, MN; Prototypes; Cherry et al. 2013), that are expelled just prior to parturition and indicate time and location of parturition events to facilitate capture of neonates at the birth site (Nelson et al *in review*). We fitted fawns with expandable, breakaway collars (Advanced Telemetry Systems; M4210), and monitored survival using a three-element yagi antenna and portable receiver (Wildlife Materials; Murphysboro, IL; TRX-2000S) ≥ 5 times weekly until 15 October. We used 3 months as a recruitment threshold because fawns are considerably less susceptible to predation after 3 months (Kilgo et al. 2012, Nelson et al. *in review*). We calculated survival of the marked population by dividing the number of surviving fawns by the total number of marked fawns, excluding those with unknown fates. We suggest that survival of our marked sample was representative of the deer population at JC because we used multiple capture methods for fawns and distributed our capture effort across the entire study site.

Data Analyses

To investigate if body mass and condition varied during the seasons we monitored fecundity, we used an linear model with age, evidence of lactation, and modified Julian date of harvest (i.e., 1-88; 20 October = 1, 15 January=88) as a covariates to test for differences in body mass among hunting season (2005-2006, 2006-2007, and 2012-2013). We used t-statistic to test the effect of independent variables in the model and develop 95% confidence intervals around coefficient estimates to evaluate mean separation among classes of categorical variables. We compared mean tail-fat indices between hunting seasons using the nonparametric Wilcoxon ranked sum test because the response variable was categorically ranked (i.e., tail fat deposition score, 1-5) and not normally distributed. We first tested for age effects to identify if age-specific analyses were required. Tail fat indices did not differ by age (X^2 =4.05, df=2, P=0.13); therefore, we pooled ages and tested the effect of hunting season on tail fat indices.

We used all harvest records from female deer ≥1.5 years collected 1 December – 15 January, during 2005-2007 (n=30) and 2012-2013 (n=20) to test for effects of coyote-deer ratios on fecundity. We set evidence of ovulation (presence of ≥1 CL) as a binary dependent variable and used maximum likelihood to fit a generalized linear mixed model (GLMM) to test the effects of coyote-deer ratios while controlling for the effects of age and a modified Julian date of harvest. We included a modified Julian date of harvest (1-46; i.e., 1 December = 1 and 15 January= 46), because the incidence of ovulation likely increased throughout the sampling period. We used records from 145 female deer ≥1.5 years of age harvested during 15 October - 15 January, 2006-2007(n=55), 2007-2008 (n=51) and 2012-2013 (n=71) to fit a GLMM with evidence of lactation set as a binary dependent variable while controlling for effects of age and date of harvest to test the effects of coyote-deer ratio on lactation. We used the Wald statistic to test significance of effects within GLMMs and included the hunting season (i.e., 2005-2006, 2006-2007, and 2012-2013) as a random effect in all GLMMs.

We captured 21 fawns during 2007-2008 and 28 fawns during 2011-2012, but censored four fawns during each period, due to collar malfunction; thus, our analysis of survival to age at recruitment included 17 and 24 fawns from periods of high and low predation risk, respectively. We assigned a fate (i.e., survived to 15 October, or expired) to each monitored fawn and calculated the proportion of radio-tagged fawns that survived during the periods of high and low predation risk. We used a logistic regression with fate as binary response variable to test for differences among high and low predation risk periods. We used hunter observation data to calculate FAF ratios for periods of high and low predation risk. To test if the number of fawns observed relative to the number of adult female deer observed was independent of period we used a chi-square analysis and Fisher's exact test. For corroboration, we also estimated FAF ratios using fecundity and survival data. We calculated FAF ratio for each period using mean number of CL per female deer multiplied by the percentage of radio-tagged fawns that survived to age at recruitment (i.e., Calculated FAF = mean number of CLs per female * proportion of radio-tagged fawns that survived to age at recruitment).

We performed all analyses using R (R Development Core Team 2011). We used $\alpha=0.05$ for all significance tests. Samples obtained from lawfully harvested deer did not require animal welfare clearance. We handled all fawns in strict accordance with the University of Georgia's Institutional Animal Care and Use Committee (Proposal Number: A2011 03-009-R2).

RESULTS

Body mass differed ($t = 2.45$, $P=0.033$) between the 2005-2006 and 2006-2007 hunting seasons but the 2012-2013 hunting season was similar ($t = 1.22$. $P=0.22$) to both earlier hunting seasons (Table 1). Body mass increased with age ($F_{2,\,172}=54.07$, $P<0.001$), but not with lactation or date of harvest. Tail fat indices differed significantly by hunting season ($X^2=8.60$, df=2, P=0.01). The greatest tail fat scores occurred during 2006-2007 hunting season (Table 1).

The proportion of females with evidence of ovulation (i.e., presence of ≥1 CL) at harvest was ([mean ± SE] 0.5 ± 0.11) during 2006-2007, (0.5 ± 0.18) during 2007-2008, and (0.8 ± 0.04) during 2012-2013 (Table 2) and negatively related to the coyote-deer ratio (Z=-2.13, P= 0.03). Evidence of ovulation increased with Julian date of harvest (Z=2.77, P=0.006); however, counter to expectations, age did not influence evidence of ovulation (Z=-0.52, P=0.61). Similarly, the proportion of adult female deer with evidence of lactation was negatively related to coyote-deer ratios (Z=-2.34, P=0.019) and Julian date of harvest (Z=-2.41, P= 0.016), but was positively related to age (Z=4.13, P< 0.001). The proportion of female deer ≥2.5 years old with evidence of lactation at harvest were (0.68 ±0.07) during 2006-2007, (0.66 ± 0.08) during 2007-2008, and 0.86 ± 0.04) during 2012-2013. In contrast, survival of radio-tagged fawns to age at recruitment did not differ (Z=0.031, P= 0.98) between periods of high predation risk (0.41 ± 0.12, n = 17) and low predation risk (0.42 ± 0.10, n = 24; Figure 2).

The number of fawns observed relative to the number of adult female deer observed was dependent on period (X^2= 4.124, df = 1, P=0.042). Hunter-observed FAF ratios during high predation risk (0.50, n = 275) were less than during low predation risk (0.80, n = 233, Figure 2). Calculated FAF ratios using fecundity and survival data followed the same trend as hunter observation data (e.g., $FAF_{(high\ risk)}$ = 0.4 = [0.9 x 0.4], and $FAF_{(low\ risk)}$= 0.6 = [1.5 x 0.4]).

DISCUSSION

Our study suggests coyotes can influence deer recruitment, independent of direct predation, through interactions that result in reduced fecundity. We documented that the proportion of females with evidence of ovulation at harvest increased following the coyote decline. Nutritional condition can influence reproduction in deer (Verme 1967, Ditchkoff 2011), but here the observed variation in fecundity was not related to changes body mass and condition. The physiologically mediated pathways, by which deer alter reproductive strategy in response to environmental conditions (e.g., weather and population density), may also be sensitive to more general environmental stressors, such as predation risk (Rhodes et al. 1985). As capitol breeders, a reduction in resources allocated to current reproduction, is an investment in nutritional condition and future reproduction (Cheatum and Severinghaus 1950; Festa-Bianchet et al. 1998; Therrian et al. 2007, 2008). Perhaps during periods of high predation risk, deer delay their investment until conditions are more favorable. Perceived predation risk is an environmental force that can influence prey demography independent of direct predation (Zannete et al. 2011), and should be considered when managing deer populations.

Only approximately 40% of fawns survived to recruitment and 76.2% of mortalities were predation events (Nelson et al *in review*), demonstrating that direct predation had profound influence on recruitment during our study. However our results support the suggestion of Patterson and Messier (2000) that predator-prey ratios may not be a reliable indicator of predation rates of deer by coyotes. We observed similar survival rates of marked fawns among periods of high and low predation risk, suggesting that changes in fawn survival were not responsible for observed variations in recruitment. Therefore, we suggest variation in recruitment is best explained by variation in fecundity. The higher ovulation rates we observed during the period of higher deer abundance indicate that there were no density-dependent reductions in fecundity within the studied population during 2012-2013. Given that reproductive fitness can be influenced by predation risk (Creel et al. 2007, Sheriff et al. 2009, Zanette et al. 2011), we think it is appropriate to conclude that decreased predation risk resulting from lower coyote-deer ratios best explains the increased ovulations rates and higher recruitment we documented during 2012-2013.

Physiological responses to predator-induced stress can cause reduced prey survival and birth rates, providing an intuitive mechanism for indirect predator effects on prey demography (Clinchy et al. 2013). There is a growing appreciation for the impacts of predator-induced stress on prey physiology and ecosystem function (Hawlena and Schmitz 2010, Travers et al. 2010, Clinchy et al. 2013). The sight or smell of predators can cause measureable physiological responses in prey (Cockrem and Silverin 2002, Campeau et al. 2008) that can have long-lasting effects even from a single exposure to a stressor (Adamec and Shallow 1993, Armario et al. 2008). Boonstra et al. (1998) demonstrated the reproduction that drives the population cycles of snowshoe hare were tied to physiological stress induced by predation risk rather than hare density or nutritional condition and subsequently, Sheriff et al. (2009) documented a correlation between fecal cortisol metabolite and litter size, and offspring body mass. Traver et al. (2010) simulated nest predation on song sparrow nests and documented decreased clutch size in successive nesting attempts and poorer physiological condition. The effects of the simulated predator stress were most evident in non-resource based physiological indices, demonstrating the potential for reduced fecundity as a result of an endocrinologic response to predator stress rather than reduced nutritional condition.

Though glucocorticoid levels vary with food intake in other species (Boonstra et al. 1998, Clinchy et al. 2004), Creel et al. (2009) suggested nutritional deficits resulting from foraging tradeoffs could result in reduced fecundity, independent of predator stress in elk. Wolf-elk ratios were negatively associated with progesterone concentration in elk feces, which is diagnostic of gestation during the third trimester in elk (Creel et al. 2007). However, fecal glucocorticoid metabolite concentrations did not differ with predator-prey ratios, supporting the predator-sensitive foraging hypothesis, which predicts antipredator behaviors restrict foraging and results in decreased nutritional condition and reproduction (Creel et al. 2009). Interestingly, others have failed to find a relationship between wolf predation risk and elk nutritional condition and pregnancy rates (White et al. 2011, Middleton et al. 2013), highlighting the complex nature of foraging-safety tradeoffs, and their effects on the interactions between nutritional condition, physiological processes, and fecundity. Predation risk can decrease reproduction in wildlife populations via numerous pathways and can have profound effects on prey populations (Sheriff et al. 2009, Creel et al. 2007, Travers et al. 2010, Zanette et al. 2011).

Reproduction in cervids is sensitive to environmental (Richter et al. 1985, Mech et al. 1987, Simard et al. 2014) and social stressors (Blanc and Thériez 1988). Reproductive behavior of female deer provides numerous opportunities for predation risk to influence parental care in ways that may increase probability of mortality from other sources, including the selection of fawn-rearing habitats, frequency and duration of feeding events, and abandonment/starvation rates. Predator-mediated foraging decisions of dams during gestation and lactation could influence fitness of offspring and population demography through decreased body mass and condition (Ditchkoff 2011). Body mass and condition has been related to fecundity in deer (Verme 1967), moose (*Alces alces*; Sæther & Haagenrud 1983), caribou (*Rangifer tarandus*; Cameron et al. 1993, 1994), roe deer (*Capreolus capreolus*; Hewison 1996, Pettorelli et al. 2002) and elk (Cook et al. 2004). We hypothesize that predators can both increase body mass of female deer by decreasing lactation costs through fawn predation, and decrease body mass of female deer through predator-sensitive foraging. These contrary predictions demonstrate why inference regarding fecundity is difficult with body mass data alone, and that non-consumptive effects of predators on prey body mass could be masked if analyses do not control for reproductive condition (Festa-Bianchet et al. 1998). Here we observed a difference in body mass among hunting seasons, but ovulation rates were similar between the year of highest (2006-2007) and lowest (2005-2006) body mass and condition. Instead, ovulation rates varied with the coyote-deer ratio, independent of body mass and condition. However, we acknowledge that our investigation of nutritional condition relied on only two relatively coarse measurements on nutritional condition (Cook et al. 2001)

We previously documented a negative relationship between adult female deer body mass at harvest and a coyote abundance index, when controlling for age and evidence of lactation during an 11 year period (Cherry et al. *in review*). We suggested those data demonstrated the potential for coyote populations to reduce the nutritional condition of deer through predator-sensitive foraging. As predicted in model described in Cherry et al. (*in review*), body mass decreased with predation risk when controlling for reproductive condition. However body mass was ultimately similar between hunting seasons of high and low predation risk because of higher reproductive costs during the low predation risk season. We observed the highest incidence of lactation at harvest during the low risk season in this study than has been previously recorded for our study site from 1992-2013 (B. T. R. unpublished data).

In this study we believe deer were able to maintain nutritional condition despite the variation in coyote-deer ratios because of abundance of resources, and that changes in fecundity resulted from physiological processes that cause deer to adjust reproductive strategies. Deer are synchronous polyestrous breeders that can cycle multiple times in a single breeding season if pregnancy is not achieved during the first estrous cycle (Mansell 1971, Ditchkoff 2011). Our samples of ovaries from adult deer were collected during the first two estrous cycles of the breeding season. While lactation and ovulation data from a single deer represent two separate breeding seasons, they remain representative of our designation of high and low predation risk periods. The lactation data (67% and 87% of adult females lactating at harvest during periods of high and low predation risk, respectively) suggest we underestimated ovulation rates (50% and 80% of adult females with evidence of ovulation at harvest during periods of high and low predation risk). We likely underestimated fecundity because some harvested deer would have ovulated during subsequent periods of estrous. However, we controlled for these effects by including a modified Julian date of harvest as a covariate in our model of ovulation success. It is possible that predation risk caused delayed reproduction, and pregnancy rates were eventually similar among periods. Other stressors, such as decreased autumn nutritional condition can cause delayed estrus in white-tailed deer (Verme 1965) and moose (Garel et al. 2009). However, under that scenario, our results would still suggest predation risk influenced breeding chronology. In deer in the southeastern USA, the probability of fawn survival decreases with increasing date of birth (Kilgo et al. 2012) and late-born fawns are less likely to achieve body size required to breed during their first winter (Ditchkoff 2011).

Our results suggest perceived predation risk, like other environmental factors, may trigger physiological processes resulting in decreased fecundity. We documented a reduction in ovulation rates that appears to be independent of nutritional condition (i.e., body mass at harvest and tail-fat deposition rates were not related to fecundity) suggesting a physiologically mediated process, yet further research is needed for a mechanistic understanding of the process. Predators can influence many aspects of deer recruitment; therefore, we recommend studies undertake holistic approaches that incorporate measures of direct and indirect predator effects to understand the totality of the effect of coyote populations on deer recruitment, and more generally predators on their prey.

CONCLUSION

Following a decline in coyote abundance from 2008 to 2011, we observed an increase in deer ovulation rates. The rapid decline in coyote abundance resulted in an increase in deer *in utero* production of >0.5 fawn per adult female, suggesting coyotes can have considerable effects on deer demographics independent of direct morality. In addition, hunter-observed FAFratios mirrored the increase in ovulation rates while survival of marked individuals remained constant. Our results suggest that deer, like elk (Creel et al 2007; 2011), snowshoe hare (Boonstra et al. 1998, Sheriff et al. 2009), grey-side voles (Olaf and Halle 2004), song sparrow (Travers et al. 2010, Zanette et al. 2011), and likely many other vertebrate species, reduce reproduction under conditions of high predation risk. Our study demonstrates that coyotes can have strong non-consumptive effects on deer populations, and ignoring these effects may result in dramatic underestimation of impacts of expanding coyote populations on ecosystems.

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Table 4.1. Age-specific lactation rates, mean body mass and tail fat indices (1-5 scale; 1-poor, 5-excellent condition), of white-tailed deer females harvested during 3 hunting seasons on the Joseph W. Jones Ecological Research Center in southwestern Georgia.

Hunting Season	Age Class	# of females harvested	Lactation (%)	Body mass (kg)		Tail fat index (1-5)	
				X	SE	X	SE
2005-2006	1.5	14	36	43.0	1.6	2.4	0.2
	2.5	23	61	49.5	0.9	2.3	0.1
	≥3.5	18	77	52.8	1.6	2.4	0.2
2006-2007	1.5	12	8	47.6	1.1	2.8	0.2
	2.5	23	65	49.6	1.1	2.7	0.2
	≥3.5	16	66	51.4	1.6	3.1	0.3
2012-20013	1.5	6	17	44.1	2.6	2.3	0.3
	2.5	34	88	49.6	1.0	2.6	0.2
	≥3.5	31	84	54.4	1.1	2.4	0.2

Table 4.2. Ovulation rates (i.e., corpora lutea [CL] counts on paired ovaries) of white-tailed deer females harvested 1 December through 15 January separated by year of harvest and age class on the Joseph W. Jones Ecological Research Center in southwestern Georgia.

Year	Age Class	Ovarian Analyses		
		# of Females examined	% of Females with ≥ 1 CL	# of CL/Female
2005-2007	1.5	9	55	1.00
	2.5	10	60	1.09
	≥3.5	11	36	0.77
2012-2013	1.5	2	100	2.00
	2.5	10	70	1.30
	≥3.5	8	88	1.30

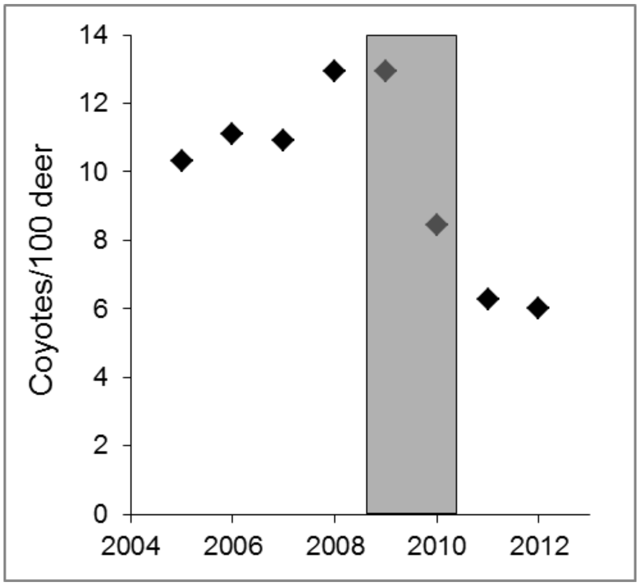

Figure 4.1. Coyotes per 100 deer ratio developed from white-tailed deer and coyote detection data from 28 1-km track count transects on the Joseph W. Jones Ecological Research Center in southwestern Georgia. The grey shaded area divides the periods of high and low coyote-deer ratios.

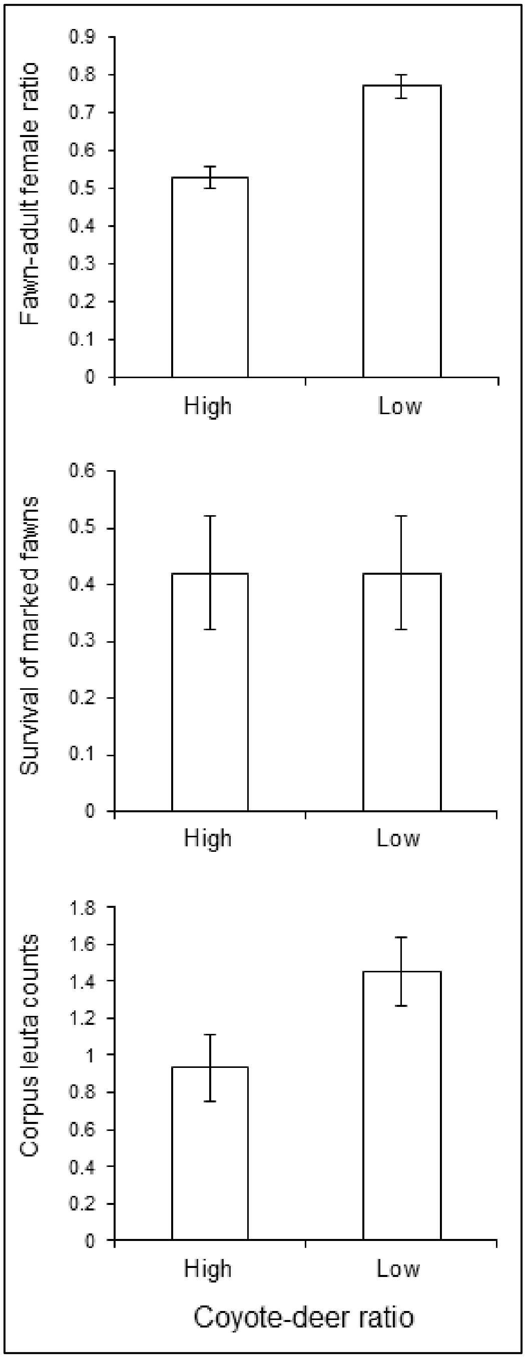

Figure 4.2. Fawn-adult female ratios, recruitment of marked individuals, and ovulation rates. (A) Hunter-observed fawn-adult female (FAF)ratios, (B) Survival of marked fawns, and (C) Ovulation rate (corpora lutea counts) of white-tailed deer harvested on the Joseph W. Jones Ecological Research Center in southwestern Georgia during high coyote abundance (2005-2007) and low coyote abundance (2012-2013) with standard error represented with error bars.

CHAPTER 5

EFFECTS OF 10 YEARS OF PREDATOR EXCLUSION ON OAK RECRUITMENT AND SELECTED DEER FORAGES IN A LONGLEAF PINE SAVANNA[4]

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[1] Cherry, M. J., L. M. Conner, and R. J. Warren. To be submitted to *Forest Ecology and Management*

ABSTRACT: In longleaf pine savannas, canopy species are “pyro-engineers” contributing litter of varying flammability to the fuel bed beneath their crowns and ultimately affecting vegetation diversity. Additionally, ecologists increasingly recognize the importance of trait-mediated indirect interactions of wildlife species on forest ecology. Therefore, we examined the role of mammalian-predator exclusion on oak regeneration and the density of palatable understory species in a longleaf pine savanna. During 2003, we identified eight, approximately 40-ha plots, and randomly selected four to receive a predator exclusion treatment, while the remaining plots served as controls. Plots received five bi-annual prescribed fires during the experiment. In 2012, we measured the density of three size classes of oaks; sprouts (cohort since fire), saplings (survived ≥1 fire and <15cm diameter at breast height [DBH]), and mature (≥15 cm DBH). The density of sprouts was 3.7 times greater ($F_{1, 5} = 28.80$, P=0.003), and the density of saplings was 2 times greater ($F_{1, 5} = 50.76$, P=0.001) in predator exclosure plots than control plots. The density of mature oaks did not affect sprout ($F_{1, 5}$=3.11 P=0.138) or sapling ($F_{1,5}$=16.28 P==0.072) density. Conversely, the density of 10 palatable understory plants was lower in predator exclosures than control plots ($F_{1, 12}$=12.69, P=0.004). We previously documented altered foraging behavior of herbivores in predator exclosures, and speculate predator exclusion influenced food web dynamics, which caused increased oak recruitment and decreased density of palatable understory plant species.

KEY WORDS: Behaviorally-mediated trophic cascade, *Canis latrans*, coyote, fire trap, longleaf pine, non-consumptive effects, oak recruitment, *Odocoileus virginianus*, predation risk, prescribed fire, trophic cascade, white-tailed deer

INTRODUCTION

Trophic cascades explain interactions between predators, and the resources their prey consume (Paine 1980). There is growing evidence suggesting predators can exert powerful top-down effects on ecosystems by influencing prey abundance and behavior (Myers et al. 2007, Estes et al. 2011, Ripple et al. 2014). Trophic cascades often arise when predators protect plants by reducing herbivore abundance; however, behaviorally mediated trophic cascades (BMTCs) can occur when predators protect plants by altering foraging behavior of prey (Beckerman et al. 1997; Schmitz et al. 2004). Experimental evidence is abundant for BMTCs in terrestrial invertebrate and aquatic systems, but is lacking for terrestrial systems involving large vertebrate predators (Shurin et al. 2002). Several observational studies have suggested BMTCs structure ecosystems following the restoration of large predators (Ripple and Beschta 2004, Fortin et al. 2005, Beyer et al. 2007, Beschta and Ripple 2009), but confounding effects due to a lack of experimental control has caused much debate regarding strength of trophic cascades in complex terrestrial systems, particularly when involving behavioral interactions (Halaj & Wise 2001; Kauffman et al. 2010, 2013; Winnie 2012; Beschta and Ripple 2013).

Yet, the BMTCs hypothesis is appealing given the abundance of evidence demonstrating predators can affect when, where, how, and on what herbivores feed (Lima and Dill 1990). Prey species respond to predation risk by altering diet selection (Beckerman et al. 1997, Banks et al. 1999), habitat selection (Werner et al. 1983, Creel et al. 2005), and vigilance rates (Hunter and Skinner 1998, Laundre et al. 2001), often at the expense of foraging (Illius & Fitzgibbon 1994, Fortin et al. 2004). Christianson and Creel (2008) demonstrated female elk (*Cervus elaphus*) decreased grazing during pulses on increased predation risk, and Creel and Christianson (2009) documented elk increased consumption of willow browse response to predation risk. This shift in foraging behavior in elk from grazing to browsing is likely a function of increased use of forested cover during increased risk (Creel et al. 2005, Fortin et al. 2005). Increased use of woody browse by elk in response to predation risk is contrary to the BMTC hypothesis proposed to explain the release of trembling aspen (*Populus tremuloides,*) cottonwoods (*Populus* spp.), and willows (*Salix* spp.) following the restoration of gray wolves (*Canis lupus*) in the Yellowstone National Park, USA (Ripple & Beschta 2004, Creel & Christianson 2009, Winnie 2012), but demonstrates a behavioral mechanism through which forage selection could induce BMTCs.

Longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) savannas of the southeastern USA are characterized by globally significant levels of biodiversity, with numerous endemic flora and fauna species (Peet and Allard 1993, Mitchell et al. 2006). As many as 50 plant species can occur in a single square meter, with >1,100 species on 11,000 ha (Drew et al. 1998, Kirkman et al. 2001). A frequent, (e.g. often 1-3 years) fire-return interval contributed to species richness by maintaining an open canopy and preventing the development of a midstory composed of fire-impeding species such as oaks (Quercus spp.), gallberry (Illex spp.) and offsite pines (i.e., *Pinus* Clausa; Glitzenstein et al. 1995, Kirkman et al. 2004). Many tree species exist in a “fire trap,” or demographic bottleneck where they repeatedly sprout after loss of aboveground biomass, but rarely escape into older size classes due to frequent fire (Grady & Hoffmann 2012). When hardwood species escape the fire trap, the midstory closes, floral and faunal diversity decrease, and fire becomes less frequent and more severe (Kirkman et al. 2004; Mitchell et al. 2006, 2009; Grady and Hoffman 2012). Oak encroachment into the midstory of longleaf pines stands adversely affects threatened and endangered species including the red-cockaded woodpecker (*Picoides borealis*) and gopher tortoise (*Gopherus polyphemus*; Walters et al. 1991, Allen et al.

2006, Mitchell et al. 2006). However, Hiers et al. (2014) recently highlighted that the predominate paradigm of restoring longleaf pine ecosystems through eradication of oaks and other fire-impeding hardwoods, fails to acknowledge the contribution of pyrophytic oaks to biodiversity.

In southeastern USA savannas, canopy species are "pyro-engineers" contributing litter of varying flammability to the fuel bed beneath their crowns (Kane et al. 2008, Ellair, & Platt 2013; Figure 1). For example, longleaf pine litter is more flammable than the litter of most hardwoods, and heterogeneity in canopy composition can cause fine-scale variation in fire intensity that can influence aboveground damage and survival experienced by understory plants, germination of legumes and grasses, and future forest conditions (Williamson & Black 1981, Rebertus et al. 1989, Thaxton and Platt 2006, Mitchell et al. 2009, Ellair, & Platt 2013, Wiggers et al. 2013). Fire and browsing can interact to influence the balance of trees and grasses in savanna systems (Scholes and Archer 1997; Higgins et al. 2000; Barnes 2001; Sankaran et al. 2004, 2005). For example, Staver et al. (2009) demonstrated that both fire and browsing reduced tree growth, but only their combined effects limited tree density in an African savanna. Aboveground fire survival of oaks in frequently burned longleaf pine savannas is a function of size of the oak at the time of fire, local fuel characteristics, and fire conditions (Glitzenstein et al. 1995, Ellair, & Platt 2013). Growth of oak saplings following fire can be affected by herbivory (Adams and Rieske 2001), and thus foraging behavior and abundance of herbivores could influence oak fire survival.

White-tailed deer (*Odocoileus virginianus*; hereafter deer) and their primary predators (i.e., cougar [*Puma concolor*], red wolf [*Canis rufus*], gray wolf, and black bear [*Ursus Americana*]; were extirpated across much of eastern North America. During the 1900s deer populations were restored through restocking efforts, but predator populations were not (Ballard

2011). In the absence of predators, some deer populations achieved densities incompatible with human interests and which could be damaging to ecosystem diversity and function (Warren 1997, Stromayer and Warren 1997, Cote et al. 2004). Deer have the potential to be highly interactive amongst trophic levels because of their susceptibility to the direct and indirect effects of predation (Cherry et al. *in review* a, Howze et al. 2009, Kilgo et al. 2012) and their ability to influence forest structure and ecosystems through herbivory (Stromayer and Warren 1997, Cote et al. 2004).

During the last half of the 20th century, coyotes (*Canis latrans*) colonized many eastern USA ecosystems that had lacked larger predators for decades (Gompper 2002), and may have induced prey behavior in deer populations that had experienced little selective pressure for antipredator behaviors in recent decades. In the longleaf pine ecosystem, predation risk has strong effects on deer space use (Cherry et al. *in review* a) and foraging-vigilance tradeoffs (Cherry et al. *in review* b). Coyotes can affect deer populations in eastern North America numerically (Patterson and Messier 2000, Howze et al. 2009, Kilgo et al. 2012) and behaviorally (Cherry et al. *in review* a, b), but the implications on plant communities is poorly understood.

Predation risk can increase ungulate use of woody browse and concealment cover (Edwards 1983, Creel et al. 2005, Creel and Christianson 2009). We predicted that predation risk would cause deer to increase consumption of oak saplings, resulting in decreased oak recruitment. Predation risk can result in an increase in the density of palatable browse species (Callan et al. 2013, Waser 2014); therefore, we predicted that the density of selected deer forage species would be higher in risky areas. We experimentally manipulated predation risk through predator exclusion, and examined the effects of 10 years of exclusion on oak recruitment and the density of selected browse species. We have previously demonstrated that deer use predator exclosures more than controls and are less vigilant when foraging in exclosures (Cherry et al. *in review* a, b). We predicted predator exclusion would alter the value of resources and increase selection for high-quality forage items and decrease selection for woody browse. We hypothesized that 10 years of predator exclusion would result in increasedoak recruitment and decreased abundance of selected browse species.

METHODS AND MATERIALS

Study Site

Our research took place on Ichauway, the 12,000-ha outdoor research site of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia, USA. Ichauway included approximately 7,250 ha of longleaf pine (*Pinus palustris*) woodlands. Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens–Nyssa biflora*) limesink ponds (Boring 2001). Management on Ichauway emphasized balancing multiple objectives, rather than maximizing the production of any one amenity (Mitchell et al. 2006). Prescribed fire was the primary management tool used to maintain the longleaf pine ecosystem on Ichauway. White-tailed deer abundance was managed through adaptive harvest to maintain densities well below carrying capacity, maintain herd health and reduce herd impacts on the ecosystem. Estimated white-tailed deer densities were between 3.8-5.8 deer/km^2 during the study (B. Rutledge, personal communication). Coyotes and bobcats (*Lynx rufus*) were the non-human predators of white-tailed deer on site (Howze et al. 2009, Nelson et al. in review).

Predator Exclusion

In 2003, we chose eight, approximately 40 ha sites of similar habitat composition (i.e., longleaf pine-dominated canopy and native ground cover) to serve as study plots, of which four were randomly selected to serve as mesopredator exclosures and the remaining four were controls. At plots chosen for mesopredator exclusion, we constructed a woven-wire (10 x 20–cm mesh) fence with electric wire attached to E2000 electrical fence chargers (Twin Mountain Fence Company, San Angelo, TX) along the top, middle, and bottom to deter mesopredators from climbing or digging under fences. Predator exclusion sites were trapped using a combination of soft-catch (Woodstream Corp., Lititz,PA) and cage (Tomahawk Live Trap Company, Tomahawk,WI) traps. Trapping efforts targeted raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), gray foxes (*Urocyon cinereoargenteus*), red foxes (Vulpes vulpes), coyotes, and bobcats (*Lynx rufus*). Captured predators were relocated just outside the exclosure. To ensure the effectiveness of the treatment, sites were trapped twice annually for the duration of the study. Predator exclosure fences were permeable to deer and smaller than deer home ranges reported in the literature (Stewart et al. 2011). Additional details on our predator exclosures and their effectiveness in excluding coyotes can be found in Conner et al. (2010). Trapping of mesopredators was conducted under Georgia state wildlife collection permit 29-WJH-13-203.

Vegetation effects: 10- years of Predator Exclusion

Oak regeneration—We tested the hypothesis that predator exclusion would lead to increased oak recruitment. Prescribed fire was applied to all sites in February-March 2003, 2005, 2007, 2009 and 2011 and approximately bi-annually for decades prior to the experiment. All experimental prescribed fires were conducted with tempertures10-25 C, relative humidity 25-70%, wind speeds 8-24 km/hour, and mixing height >600 m. All prescribed fires were conducted by the same burn team and using standardized prescribed fire techniques. Our objective was to evaluate the effect of predator exclusion on oak recruitment We used two measures of oak recruitment: (1) density of sprouts, which were the cohort of oaks that sprouted since the previous fire; and (2) density of saplings that were assumed to have sprouted during the experiment and survived ≥ 1 prescribed fire. We conducted surveys in July 2012, 17 months following the 2011 prescribed fire, when the cohort of sprouts since fire was easily distinguished from those that sprouted following previous fires. We assumed trees < 15 cm diameter at breast height (DBH) had sprouted since 2003, and considered trees ≥ 15 cm DBH to be reproductively mature trees. We used 15 cm as a threshold based on an estimate of 10-year growth potential of oaks across a range of site conditions (S. Jack, personal communication). Our survey included all living specimens of family *Quercus*, excluding live oak (*Q. virginiana*) and sand live (*Q. geminata*), because we seldom observed browsing on these species. We hypothesized *a priori* that traits unique to these species relative to other *Quercus* spp. in the system would limit the effects of herbivory on their distributions and recruitment. Observed oaks included *Q. nigra, Q. falcata, Q. incana Q. hemisphaerica Q. laevis.*

We used ArcGIS 9.3 (ESRI, Redlands, Ca) to randomly generate 30 points within each predator exclosure and control plot (n=240) constraining point generation to ≥100 m from the perimeter of the plot to avoid edge effects (Lashley et al. 2014). At each point we measured the distance (decimeter) to the nearest representative of three size classes of oaks; sprouts (i.e., sprouted after 2011 prescribed fire), saplings (larger than sprout and < 15 cm DBH), and mature (≥15 cm DBH). Before analysis, we examined the distance to sprouts and saplings data for outliers, and removed 5 of 240 (2%) data points that were >6 standard deviations from the mean. The removed points contained large distances to sprouts, saplings, and mature trees because the locations fell in closed canopy cypress swamps where oaks were not common. We calculated plot mean distance to each size classes of oak and transformed the mean to plot density estimates. We calculated the area of a circle with a radius equal to the plot mean distance, and considered that a measure of 1 tree per circle of a given area in cm^2. We then converted density estimates to trees per ha. We considered the plot the experimental unit (N=8) and used analysis of variance (ANOVA) to test for differences in sprout and sapling densities among predator exclosure and control plots, while including the density of mature oaks as a covariate. We tested for normality using a Shapiro-Wilk normality test and assigned significance at $\alpha=0.05$.

Selected deer forage species—We identified four genera (i.e., *Desmodium* spp., *Lespedeza* spp., *Rubus* spp., and *Smilax* spp.) and six species (i.e., *Acalypha rhomboidea, Ambrosia artemisiifolia*, *Centrosema virginianum*, *Chamaecrista fasciculata*, *Rhynchosia reniformis*, and *Stylosanthes biflora*) common in longleaf pine-dominated upland stands on Ichauway (K. Kirkman, unpublished data) and selected by white-tailed deer (Warren and Hurst 1981, Miller and Miller 1999). We established three 180 m transects, with 12, 1-m^2 subplots separated by 15 m in focal monitoring stands within each plot. Focal monitoring stands were characterized by a longleaf canopy and native groundcover and were established at the onset of the experiment based on habitat similarity. We documented the occurrence of 10 deer forage species in each subplot during August of 2011 and 2012, and developed plot means representing the number of deer forage species per m^2 for each year (N=16). We used an ANOVA to test for differences in density (species per m^2) of deer forage species among predator exclosure and control plots. The 2011 and 2012 surveys were conducted six and 18 months post-fire. Vegetation structure and species composition can differ considerably with time since fire, therefore we included year, and a predator exclosure x year interaction as independent variables. We tested normality of all models using a Shapiro-Wilk normality test and assigned significance at $\alpha=0.05$. All analyses were conducted in Program R (R Development Core Team 2011).

RESULTS

The density of spouts was greater ($F_{1,5}$ = 28.80, P=0.003) in predator exclosure plots (Mean ± SE; 80.60 ± 11.52 trees per ha) than control plots (21.80 ± 5.46 trees per ha; Figure 2). Similarly, the density to saplings was greater ($F_{1,5}$ = 50.76, P=0.001) in exclosure plots (15.38 ± 5.33 trees per ha) than control plots (7.52 ± 2.57 trees per ha). The density of mature oaks did not affect the density of sprouts ($F_{1,5}$=3.11 P=0.138) or saplings ($F_{1,5}$=16.28 P==0.072).), Density of selected deer forage species (Figure 3) was lower ($F_{1,12}$=12.69, P=0.004) in predator exclosures (2.00 ± 0.17 species per m^2) than control plots (3.00 ± 0.22 species per m^2). There was no effect of year or predator exclusion treatment x year interaction on selected species abundance.

DISCUSSION

Predator exclusion increased oak recruitment and decreased the density of selected deer forage species in a frequently burned longleaf pine savanna. We document a variation in vegetation after 10 years of predator exclusion in a frequently burned system, demonstrating that predation effects can cascade to plant communities by enhancing effects of fire. That is, frequent fire created a demographic bottleneck for oaks (Grady & Hoffman 2012), and predator risk influenced the strength of the process. Our results suggest predators reduced oak recruitment. In longleaf pine savannas oak encroachment into the midstory reduces floral and faunal diversity and adversely affects threatened and endangered species including the red-cockaded woodpecker and gopher tortoise (Walters 1991, Kirkman et al. 2004, Allen et al. 2006, Mitchell et al. 2006

We documented an increase in oak recruitment in predator exclosures, suggesting that deer, like elk, increase consumption of woody browse under risky conditions (i.e., control plots; Morgantini and Hudson 1985, Christianson and Creel 2008, Creel and Christianson 2009). Predation risk causes many prey species to increase use of habitats that provide concealment cover (Werner et al. 1983, Creel et al. 2005). In longleaf savannas, unburned patches (i.e., thickets of Harcombe et al. 1993; oak domes of. Guerin 1993) create refuge for oak regeneration and form dense thickets that provide concealment cover from predators (Grady and Hoffmann 2012, Hiers et al. 2014). We speculate that predation risk likely increased use of patches providing concealment cover, resulting in increased use of oaks. Additionally, deer may increase use of oaks under higher risk conditions, such as prevailed in our control plots, because oaks require a low search time due to greater height than most understory plants in biannually burned longleaf pine stands. Further, deer can browse oak saplings at a height allowing a more vigilant posture while foraging. We suggest oak saplings represent a "safe" food resource and should be utilized more during high risk conditions, because they are often associated with concealment cover, have a low search time, and can be exploited in a vigilant posture. Conversely, we speculate that in prey refugia, such as prevailed in our predator exclosures, the value of oak browse as a resource decreases and deer bypass "safe" food items and increase selectivity for high-quality food items. The deer forage species we surveyed were often entangled in a dense ground cover layer that could have as many as 50 species in a square meter (Drew et al. 1989, Kirkman et al. 2001). We assume these species provide a high reward, but require more search effort than oak saplings. Increasing search time has different cost under high and low risk conditions (Brown et al. 1999). In the absence of predators the cost of search time is reduced and the value of the selected forage species increases, while the benefit of a quick meal is appreciated in the presence of predators.

The hypotheses tested in this study were based on previous work demonstrating deer were less vigilant and more often detected in predator exclosure plots than control plots (Cherry et al. *in review* a, Cherry et al. *in review* b). By creating predator exclosures that were smaller than a typical home range for a deer (Stewart et al. 2011) and which deer frequently crossed, we isolated the behavioral effects of predator exclusion because both our control plots and exclosures were available to the same population of deer. However, it is possible that the vegetation changes we documented in this study may have been influenced by other changes in the wildlife community in response to our predator exclosure treatments. Several other concomitantly conducted research projects on our control plots and exclosures demonstrated that predator exclusion did not affect survival of cotton rats (*Sigmodon hispidus*, Morris et al. 2011a), two species of Peromyscus (Morris et al. 2011 b), or southern flying squirrels (*Glaucomys volans;* Karmacharya et al. 2013). However, predator exclusion did influence space-use of cotton rats (Morris et al. 2011 c), suggesting potential for a behavior-mediated mechanism involving rodents. Gopher tortoise recruitment also increased in predator exclosures (Smith et al. 2013). Gopher tortoises may influence plant communities through herbivory or through soil disturbance associated with burrowing and locomotion. We suggest there are many potential interconnected pathways for predator exclusion to influence a plant community, and their combined effects may have contributed to the change in vegetation we documented.

Restoration of carnivores is often justified by the restoration of trophic cascades, but experimental evidence involving large terrestrial predators is rare. Ripple et al (2013) document the negative effects of coyote expansion following wolf declines in western North America, however, if coyote populations are capable of reducing deer abundance (Kilgo et al. 2010), and restoring an ecology of fear (Brown et al. 1999, Cherry et al. *in review* a,b) to deer populations in eastern North America, then the relief from herbivore pressure would be welcomed in many systems that have been degraded during the past few decades by overabundant and fearless deer (Warren 1997; Cote 2004). We documented BMTCs by manipulating foraging behavior of white-tailed deer through experimentally altering predator distributions. We identified predator mediated food web dynamics that provide behavioral feedbacks that could contribute to the conservation and restoration of longleaf pine ecosystems. Future research should investigate the mechanisms driving these changes and document how disturbance and predator-sensitive foraging may interact to influence ecosystems.

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Figure 5.1. The left panel is an illustration of “pyro-engineering” of fire-impeding species in a longleaf pine savanna and demonstrates how variation in fire severity can influence forest structure. The time since fire in this unburned patch will be two years greater than the surrounding stand. The right panel is an illustration of the interface between a pine savanna and an unburned patch that has escaped several fire cycles. Note the top-killed hardwoods stems in the foreground. The expansion and contraction of these unburned patches is driven by the fire survival of fire impeding species on the perimeter of the patches.

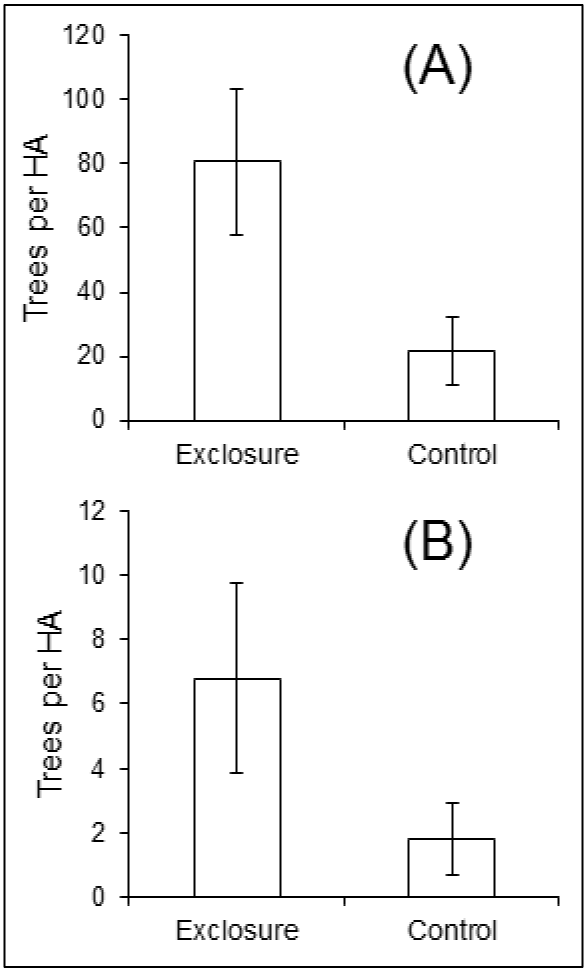

Figure 5.2. Mean density of oak (*Quercus* spp.) (A) sprouts and (B) saplings in predator exlosures and control plots at the Joseph W. Jones Ecological Research Center after 10-years of predator exclusion in southwestern Georgia, USA. Error bars represent 95% confidence intervals.

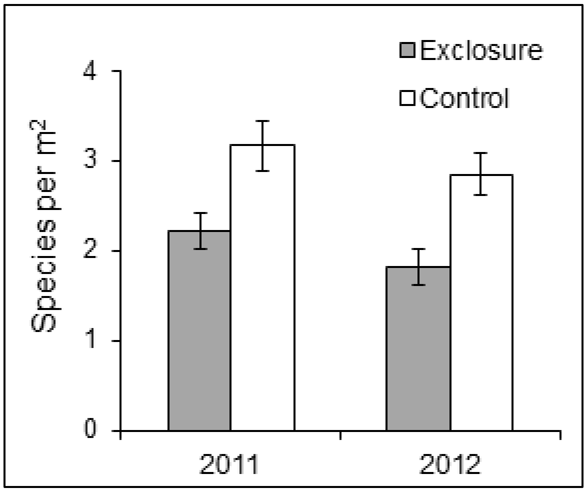

Figure 5.3. Mean number of 10 selected deer forage species per square meter, during 2011 and 2012 in predator exclosure and control plots on the Jones Ecological Research Center in southwestern Georgia, USA. Error bars represent 95% confidence intervals.

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Coyotes have recently achieved abundances in the southeastern USA capable of influencing white-tailed deer (*Odocoileus virginianus*) recruitment and demography (Saalfeld and Ditchkoff 2007; Kilgo et al. 2010, 2012, McCoy et al. 2013). I offer evidence that the interactions between coyotes and white-tailed deer transcend neonate predation and have profound effects on behavioral ecology of white-tailed deer. I combine results from experimentation using predator exclusion and correlative evidence form the examination of long-term population monitoring, to conclude that there is great potential for coyotes (*Canis latrans*) to influence white-tailed deer populations independent of direct killing.

Predator exclusion strongly influenced the foraging behavior of white-tailed deer. I documented more than twice as many detections of white-tailed deer in predator exclosure plots than control plots using thermal camera surveys and track count station monitoring data during an eight-year period. I demonstrated that manipulated predator distributions influenced white-tailed deer distributions, providing experimental evidence that white-tailed deer space use was influenced by perceived predation risk. Further, white-tailed deer spent more time feeding while at baited camera traps in exclosures than control plots. Surprisingly, predator exclusion had a more pronounced effect on males than females, but both sexes showed strong seasonal effects. Predators had the strongest effect on the foraging behavior of males during post-rut and on females during the fawning season. This work provides experimental evidence that predators can influence white-tailed deer foraging behavior.

Like most prey species, ungulates evolved with many adaptations to reduce the risk of predation and to mitigate the activity costs associated with antipredator responses. For example, ungulates can compensate for increased vigilance while foraging, by increasing total time spent foraging to achieve daily energetic requirements. Further vigilance can have no cost when intake rate is limited by food handling rather than food encounter (Illius, and FitzGibbon 1994). While there is an activity cost associated with any shift in time allocation, the costs may be inconsequential to prey fitness or trophic level interactions. Therefore, to investigate the ecological relevance of the observed antipredator responses, I investigated the effects of these behaviors on white-tailed deer nutritional condition, fecundity, and recruitment using long-term population monitoring, harvest data, and monitoring survival of marked fawns.

I documented a negative relationship between coyote abundance and body mass of harvested adult female white-tailed deer, while controlling for age and reproductive condition. I found no support for other ecological variables that might have affected resource availability (e.g., white-tailed deer abundance, growing-season rain). I then exploited a decline in coyote abundance and concurrent increase in white-tailed deer abundance that occurred during a 7-year period to conduct a “natural” experiment investigating the effects of predator-prey ratios on white-tailed deer fecundity. I summarized white-tailed deer nutritional condition data, multiple measures of female deer reproductive condition, survival of marked fawns, and hunter observation data to elucidate the relative contributions of direct and indirect effects of predation on white-tailed deer recruitment. I found a negative correlation between ovulation rates and predator-prey ratios. Similarly, Creel et al. (2007), demonstrated predator-prey ratios reduced pregnancy rates in elk (*Cervus elaphus*). Body mass was similar between periods of high and low predator-prey ratios, despite increased nutritional cost associated with higher rates of reproduction. These results demonstrate how predator effects (or the effects of any other environment force) on body mass could be masked if changes in reproduction are not considered. These results suggest that white-tailed deer, like elk (Creel et al 2007; 2011), snowshoe hare (*Lepus americanus*; Boonstra et al. 1998, Sheriff et al. 2009), grey-side voles (*Clethrionomys rufocanus*; Olaf and Halle 2004), song sparrow (*Melospiza melodia*; Travers et al. 2010, Zanette et al. 2011), and likely many other vertebrate species, reduce reproduction under conditions of high predation risk.

I evaluated plant communities in predator exclosure and control plots to investigate the effect of 10 years of predator-sensitive foraging on oak recruitment and density of selected deer forage species. I documented increased oak recruitment and decreased density of deer forage species in predator exclosures relative to control plots. These results suggest predator exclosures altered herbivore foraging behavior, inducing cascading effects to lower trophic levels. The Stoddard-Neel approach to ecological forestry emphasizes the use natural processes to achieve healthy forest systems (Mitchell et al. 2009). Predator-sensitive foraging is a natural process that may result in herbivory patterns that influence the distribution of fuels and future forest conditions. For example, predator-sensitive foraging reduced oak recruitment in the longleaf pine (*Pinus palustris*) savanna under study. In longleaf pine ecosystems, oaks (*Quercus* sp.) contribute to diversity and provide resources and concealment cover for many wildlife species, but if oaks become overabundant, then the fire ecology changes and floral and faunal diversity decrease (Mitchell et al. 2006, Hiers et al 2014). Therefore, factors that influence oak recruitment are of considerable interest to managers of longleaf pine systems. I suggest there is potential to use coyote predation risk to manipulate the influence of white-tailed deer herbivory and thereby promote the conservation and restoration of longleaf pine ecosystems.

Predation risk is a manageable environmental force that has strong effects on prey populations and trophic level interactions. Cromsigt (2013) recently suggested managers should consider manipulating perceived risk to alter ungulate behavior to minimize human-wildlife conflict. Coyote predation risk can be managed to manipulate foraging behavior of white-tailed deer. For example, coyote removal may increase foraging efficiency where management objectives include maximizing nutritional condition of white-tailed deer. Conversely, increased risk could be used to alter behavior where herbivore effects are not desired. I offer multiple lines of evidence suggesting coyote predation risk may influence white-tailed deer foraging behavior, population demography, and trophic level interactions. However, the complexities of coyote-white-tailed deer interactions remain poorly understood. Linking foraging theory to the vast body of research on white-tailed deer herbivory effects on forested systems offers interesting avenues for research that could have significant implications for forest management.

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