HUMAN PREDATION RISK EFFECTS ON ADULT, MALE WHITE-TAILED DEER ANTIPREDATOR BEHAVIOR

By

Andrew Richard Little

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife Ecology
in the Department of Wildlife, Fisheries, and Aquaculture

Mississippi State, Mississippi

December 2011

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By

Andrew Richard Little

Approved:

Stephen Demarais Professor of Wildlife Ecology (Director of Thesis)	Kenneth L. Gee Senior Wildlife Research Specialist The Samuel Roberts Noble Foundation (Committee Member)
Samuel K. Riffell Associate Professor of Wildlife Ecology (Committee Member)	Eric D. Dibble Professor of Aquatic Sciences (Graduate Coordinator)
Bruce D. Leopold Professor of Wildlife Ecology and Department Head (Wildlife, Fisheries, and Aquaculture)	George M. Hopper Dean (College of Forest Resources)

Name: Andrew Richard Little

Date of Degree: December 9, 2011

Institution: Mississippi State University

Major Field: Wildlife Ecology

Major Professor: Dr. Stephen Demarais

Title of Study: HUMAN PREDATION RISK EFFECTS ON ADULT, MALE WHITE-TAILED DEER ANTIPREDATOR BEHAVIOR

Pages in Study: 103

Candidate for Degree of Master of Science

Recreational hunters play an important role in managing white-tailed deer (*Odocoileus virginianus*); however, the potential for deer to alter behaviors to avoid hunters has not been addressed within the risk-allocation hypothesis. I evaluated magnitude (i.e., hunter density) and temporal variation (i.e., time of day and initial and prolonged exposure) in human predation risk on movements, resource selection, and observation rates of 37 adult male deer in southern Oklahoma. Deer recognized human predation risk by increasing diel path complexity and use of security cover with greater hunter density. Moreover, deer reduced movement rates and tortuosity while seeking out areas with security cover during prolonged exposure. However, tortuosity and use of security cover remained elevated with greater hunter density. These alterations in behaviors subsequently led to a decrease in observation rates during prolonged exposure. My results clearly support the predation risk-allocation hypothesis by the behavioral responses observed with greater hunter density.

Key words: human predation risk, risk-allocation hypothesis, *Odocoileus virginianus*

DEDICATION

This thesis is dedicated to my entire family: my wife Laura, parents Durand and Jane, and Grandmother Jewell. They all deserve credit for whom and where I am today. Most importantly, I dedicate this thesis to my Lord and Savior, Jesus Christ. He has walked with me through the ups and downs of life, and no matter what, I could always trust that He would be there for me. Thank you to my entire family and to my Lord and Savior, Jesus Christ, for your love and support throughout the pursuit of my M.S. degree.

ACKNOWLEDGEMENTS

I would first like to thank my advisor, Dr. Stephen Demarais, for his unwavering support and guidance over the past few years. You have prepared me for the next step in life as I continue my educational career and for this I am forever grateful. I am thankful for my committee members, Ken Gee and Dr. Sam Riffell, who provided me with invaluable technical guidance during this project. A special thank you to my great friend and colleague, Dr. Stephen Webb, for your unwavering support and guidance during this thesis. Furthermore, I would like to thank Josh Gaskamp for his tireless effort spent afield marking hunting compartment boundaries, trapping deer, etc. I also thank Dr. Jerry Belant, for stimulating my mind regarding predator-prey relationships. I greatly appreciate the statistical guidance provided by Dr. Bronson Strickland and Dr. Guiming Wang.

I would like to thank the Mississippi State University and the Samuel Roberts Noble Foundation for providing financial support for this research. I am grateful to all Samuel Roberts Noble Foundation employees, family, and friends who assisted with this project, capture of deer, and data collection;, particularly, Russell Stevens, Frank Motal, Chan Glidewell, Keith Klement, and Dillon Payne. Last, but not least, I would like to thank the graduate students, faculty, and staff in the Department of Wildlife, Fisheries, and Aquaculture for their support and guidance over the past few years.

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CHAPTER I

INTRODUCTION

The role of human predation is very important to conservationists as humans replace large carnivores as the top predator worldwide. Moreover, recreational hunters fill this role of top predator of white-tailed deer (*Odocoileus virginianus*) across much of North America. Top predators can influence community structure and dynamics through lethal or nonlethal effects (Schmitz et al. 1997, Ripple and Beschta 2004, Hebblewhite et al. 2005). Lethal effects may arise from predators preying on herbivores, thereby decreasing abundance of herbivores, with subsequent impacts on plant communities. Alternatively, nonlethal effects may arise when prey shift distribution and resource selection in response to predation risk (Lima and Dill 1990, Schmitz et al. 1997, Schmitz 1998). Where humans have replaced large carnivores as sole predators, predation risk effects also may result from recreational hunting (Ripple and Beschta 2004). Understanding how recreational hunting affects prey behavior will extend our knowledge of predator-prey interactions and aid in developing effective management programs.

Previous research has examined effects of recreational hunting on white-tailed deer spatial ecology (Van Etten et al. 1965, Root et al. 1988, Karns 2008); however, these projects have not examined responses within the context of predation risk assessment. Prey have evolved antipredator responses to generalized, threatening stimuli, such as loud

noises and rapidly approaching objects. Thus, when encountering disturbance stimuli, such as humans, animals will respond similarly to prey encountering a predator (Frid and Dill 2002). Wildlife must learn to assess potential risk levels to reduce encounters with predators. For example, behavioral options that maximize energy intake and increase access to mates also may expose prey to an increased risk of predation (Lima and Bednekoff 1999). Thus, risk assessment can be a major selective force in the evolution of morphological and behavioral characteristics of animals, including prey behavior (Lima and Dill 1990, Ferrari et al. 2009).

Ethologists have learned much about antipredator decision-making by observing rapid response of prey to changes in predation risk (Lima and Bednekoff 1999). However, temporal variation in risk not often accounted for when observing antipredator decision making (Sih and McCarthy 2002). This led Lima and Bednekoff (1999) to develop the predation risk-allocation hypothesis, which accounts for the magnitude and temporal variation in risk. Depending on the environment (e.g., risky or safe), prey will behaviorally adapt to the magnitude and temporal variation in risk. For example, if prey experience only brief pulses of risk in a safe environment then during these risky times prey should reduce activity and foraging. Conversely, prey living in a risky environment should drastically increase activities and foraging during brief periods of safety. However, if risk levels stay elevated for an extended period of time then prey are left with the choice of dying or increasing activity and foraging during risky times to meet energy requirements.

Predation risk assessment is central to the lives of most species (Barbosa and Castellanos 2005), thus framing our research questions under the predation risk-

allocation hypothesis provides a strong foundation for conducting this study. Animals may respond to predation risk with increased vigilance, decreased foraging, and shifts into habitats that reduce rates of detection or attack by predators (Ydenberg and Dill 1986, Lima and Dill 1990). These responses influence predation rates and can have important impacts on species interactions, including competition among prey (Werner 1991, Kotler et al. 1994, Sih and McCarthy 2002). Furthermore, understanding how white-tailed deer respond to predation risk and how they allocate time spent in low- and high-risk situations will advance our behavioral knowledge of prey response to imminent threats.

Previous research examining effects of hunting pressure on deer spatial ecology have found conflicting results. Older studies using VHF telemetry found a decrease (Dasmann and Taber 1956), whereas another found increased deer movements and home range size during the hunting season (Van Etten et al. 1965). Karns (2008) recently used GPS technology, but found no noticeable behavioral changes in adult male deer during hunting season, which may be due to insufficient sample size (n = 9) and/or low hunter pressure (0.05 hours/ha/day). Although these studies provide descriptive data of movement and home range changes due to human hunting, they do not fully address why these results occurred. Taking predation risk assessment into consideration is necessary to understand these changes.

In recent years, researchers have extended knowledge of predation risk by evaluating the temporal pattern of risk and its effect on antipredator response (Lima and Bednekoff 1999, Sih and McCarthy 2002, Gude et al. 2006, Mirza et al. 2006). This framework provided me the opportunity to explicitly test how white-tailed deer respond

to differing hunter densities throughout the hunting season. Previous studies examined general impacts of hunting on movements and refuge use but did not test specific density levels, which may be due to limited or infrequent hunting pressure (Kilgo et al. 1998, Karns 2008). One study did examine hunter density (1 hunter/8 ha), but their sample size contained 5 deer that were harvested during the project (Marshall and Whittington 1969). Currently, no other project has examined effects of specific hunter density levels on adult male deer response to human hunting risk.

My research was designed to understand how the magnitude and temporal variation in risk levels affected white-tailed deer movements, changes in resource selection, and hunter observation rates as an index to harvest susceptibility. I evaluated how 3 risk levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha), 2 temporal periods of risk (diurnal = 6 a.m. - 6 p.m.; nocturnal = 6 p.m. - 6 a.m.), and 2 exposure periods (initial hunting season = days 1-3; prolonged hunting season = days 4-13) affected the dependent variables. Treatments were intended to reflect common low and high hunter densities typical of south-central Oklahoma.

First, I examined movement behaviors by testing the hypothesis that male deer would decrease diurnal movement patterns while increasing nocturnal movements under conditions of increasing predator density and decrease site-fidelity during prolonged exposure to human predation risk (Chapter 2). Second, I hypothesized that deer will seek landscape features, which distance them or hide them from hunters during prolonged exposure (Chapter 3). Third, I compared proportion of male deer susceptible to harvest at low- and high-risk levels during initial and prolonged hunting exposure. I hypothesized that hunter observations would be greater in the high-risk level relative to low-risk, but

that observations would decline in both risk levels during prolonged exposure (Chapter 4).

Understanding the role human predation plays in nonlethal behavioral decision-making by prey species will extend our knowledge of top-down regulation in an ecosystem. Furthermore, my research will increase our understanding of how humans specifically influence predation-risk assessment of a large mammal. Lastly, with the loss of top carnivores worldwide, gathering insight about prey response to humans will aid researchers and land managers to develop more effective management programs.

LITERATURE CITED

Barbosa, P., and I. Castellanos, editors. 2005. Ecology of predator-prey interactions. Oxford University Press, Inc., New York, New York, USA.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143-164.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1-16.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications 16:285-298.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

Karns, G. R. 2008. Impact of hunting pressure on adult male white-tailed deer behavior. Thesis, North Carolina State University, Raleigh, USA.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359-1364.

Kotler, B. P., Y. Ayal, and A. Subach. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia 100:391-396.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649-659.

Marshall, A. D., and R. W. Whittington. 1969. A telemetric study of deer home ranges and behavior of deer during managed hunts. Proceedings of the Southeast Association of the Game and Fish Commission 22:30-46.

Mirza, R. S., A. Mathis, and D. P. Chivers. 2006. Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. Ethology 112:44-51.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Root, B. G., E. K. Fritzell, and N. F. Giessman. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin. 16:145-151.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78: 1388-1399.

Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. American Naturalist 327-342.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437-443.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59-73.

Werner, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. Ecology 72:1709-1720.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advanced Study Behaviour 16:229-249.

CHAPTER II

ALTERED MOVEMENT PATTERNS OF A LARGE MAMMAL EXPOSED TO VARYING LEVELS OF HUMAN PREDATION RISK

ABSTRACT

Recreational hunters have largely replaced natural predators of white-tailed deer (*Odocoileus virginianus*) across much of North America; however, the potential for deer to alter movement patterns in response to human predation risk has not been evaluated within the context of the risk-allocation hypothesis. I evaluated movement patterns of 37 adult (≥ 2.5 years) male deer at 3 risk levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha), 2 temporal periods of risk (diurnal = 6 a.m. - 6 p.m.; nocturnal = 6 p.m. - 6 a.m.), and 2 exposure periods (initial = days 1-3; prolonged = days 4-13) on a 1,861-ha study area in Oklahoma during the 2008 and 2009 rifle deer seasons. Season-long tortuosity of deer movements in the high-risk treatment was 5-fold greater than no and low-risk treatments. Movement rate declined 24% among all treatments following initial hunting exposure, and the decline was almost twice as much during night compared to day. Tortuosity declined 59% among all treatments following initial hunting exposure. Decline in tortuosity was most pronounced during nocturnal hours. Deer decreased probability of use of hunted treatments during prolonged hunting exposure by only 6.9%. Reduction of movement rates among all treatments and

increase in tortuosity with greater predator density while maintaining high site-fidelity provide evidence that deer altered movement patterns to minimize predation risk from hunting. My results support the predation risk-allocation hypothesis by the altered movement behaviors in the high-risk treatment; however, low-risk treatment was below the magnitude of risk threshold needed to illicit significant changes in movement behaviors.

INTRODUCTION

Predation has long been implicated as a major selective force in the evolution of morphological and behavioral characteristics of animals (Lima and Dill 1990, Ferrari et al. 2009). Selective pressures have changed over time for ungulates with the elimination of large carnivores and replacement by human hunters (Ripple and Beschta 2004). However, Frid and Dill (2002) suggest that prey approached by humans likely respond similarly to those approached by other predators. Although hunters must fill the predatory role to effectively manage white-tailed deer in much of North America, little information exists on whether hunters cause deer to alter movement patterns to avoid risk of predation.

Theoretical models and empirical studies suggest that animals modify antipredator decision-making to account for predation risk by reducing activities and increasing use of safer microhabitats (Sih 1987, Lima and Dill 1990, Lima 1998). However, reduction in activities and increased use of safer microhabitats can lead to important ecological issues such as increased resource competition among animals (Kotler et al. 1994, Van Buskirk and Yurewicz 1998). Thus, these responses lead to the

expectation that animals should be able to weigh the risk of predation against various benefits when deciding which behavioral option to pursue (Lima and Bednekoff 1999).

Lima and Bednekoff (1999) recognized that theoretical models and empirical studies examining antipredator behaviors did not account for temporal variation in risk, which is an unavoidable aspect of most natural environments. This led them to develop the predation risk-allocation hypothesis, which accounts for the magnitude and temporal variation in risk. For example, if prey experience only brief pulses of risk in a safe environment then during these risky times prey should reduce activity and foraging. Conversely, prey living in a risky environment should drastically increase their activities and foraging during brief periods of safety. However, if risk levels stay elevated for an extended period of time then prey are left with the choice of dying or increasing activity and foraging during risky times to meet energy requirements.

Animal response to human predation risk varies greatly depending on the type of risk, environment and temporal scale (Dasmann and Taber 1956, Van Etten et al. 1965, Kammermeyer and Marchinton 1975, Kilgo et al. 1998, Karns 2008). A common metric used to evaluate animal response to predation risk within these various conditions is examination of movement behaviors (Miller et al. 2006, Tarlow and Blumstein 2007, Stankowich 2008). My research evaluated animal response to human predation risk under the predation risk-allocation hypothesis by accounting for significant sources of variation in risk, which provides a strong theoretical framework relative to other studies examining effects of hunting pressure on deer movement patterns. To examine movement rates and tortuosity metrics under this hypothesis, I accounted for the magnitude of risk by using multiple levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1

hunter/30 ha) and temporal variation in risk during daylight hours (6 a.m. - 6 p.m.) when hunters were present and during nocturnal hours (6 p.m. - 6 a.m.) when hunters were absent. To determine if deer can discriminate between changes in magnitude and temporal variation of human predation risk, I evaluated deer movement behaviors during an initial exposure period (days 1-3 of season) and prolonged exposure period (days 4-13 of season); (Ferrari et al. 2009).

My research was designed to quantify how adult male deer perceive and respond to human predation risk during the hunting season. Based on the predation risk-allocation hypothesis, I hypothesized that adult male deer would decrease diurnal movements and increase nocturnal movements with increasing predator density during prolonged exposure. Conversely, I hypothesized diurnal tortuosity would increase while nocturnal tortuosity decreased with increasing predator density during prolonged exposure. Lastly, I hypothesized that deer would shift their use from hunted to non-hunted treatments to reduce the risk of predation during prolonged exposure.

STUDY AREA

I conducted this study on the Samuel Roberts Noble Foundation Oswalt Ranch (NFOR) in Love County located in south-central Oklahoma (Figure 2.1). The NFOR consists of 1,861 ha in the Cross Timbers and Prairies ecoregion, and is vegetated by oaks (*Quercus* spp.), elms (*Ulmus* spp.), hickories (*Carya* spp.), ashes (*Fraxinus* spp.), hackberries (*Celtis* spp.), osage orange (*Maclura pomifera),* bluestems (*Andropogon* spp.), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans)*, and numerous forbs (Gee et al. 1994). The NFOR is rurally located, with minimal road density (1.4

km/km^2) bounding and within the study area. Elevation ranges from 233 m to 300 m and slope ranges from 0 degrees to 41 degrees across the study area (U.S. Department of Agriculture-National Cartography and Geospatial Center). During 2008 and 2009 study periods, rainfall ranged from 0 to 0.41 cm and average temperature was 6.9° C (Burneyville, OK; Oklahoma Mesonet). During the study, NFOR was a non-operational ranch with no cattle grazing or prescribed fire management. Lease hunting ($\bar{x}$ = 5 hunters) ended after the 2006 hunting season to minimize effects of previous hunting exposure on study animals. Coyotes (*Canis latrans*) occurred on the study area.

The NFOR was broken into no risk (control; 679 ha), low-risk (1 hunter/101 ha; 585 ha), and high-risk (1 hunter/30 ha; 583ha) treatments based on existing landscape features, property boundaries, and fencing, with the goal of producing 3 areas of similar size and vegetative composition (Figure 2.1). Percentage cover of forest, mixed forest/grassland, and grassland was similar within the control, low-risk, and high-risk treatments. I divided the low- and high-risk treatments into smaller hunter compartments comparable to the desired risk levels, which distributed hunter effort uniformly within each treatment. I randomly relocated treatments during the second year, which shifted the treatments clockwise to create temporal replication (Morrison et al. 2010). Surrounding properties had a variety of hunting effort applied each year, ranging from none to high-risk.

METHODS

Capture and Handling

I captured 52 adult male white-tailed deer (≥ 1.5 years of age) during winters of 2008 (n = 25) and 2009 (n = 27) using drop nets (Gee et al. 1999). I aged deer according to tooth replacement and wear (Severinghaus 1949), but due to variations in wear patterns (Gee et al. 2002), I classified them as ≥ 1.5 years at capture, and all deer were ≥ 2.5 years of age by the study period. I sedated deer with an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Kreeger 1996). Prior to release, I weighed, ear-tagged, and affixed each deer with a GPS collar (ATS G2000 Remote-Release GPS, Advanced Telemetry Systems, Isanti, MN). The Institutional Animal Care and Use Committee at Mississippi State University approved all capture, handling, and marking techniques (Protocol 07-034).

Collars acquired location estimates every 8 minutes from 7 November through the study period (6 December 2008 and 7 December 2009). Each location included Universal Transverse Mercator coordinates, date, time, fix status, position dilution of precision, and horizontal dilution of position. A mortality sensor indicated inactivity after 8 hours. I monitored deer once monthly from 1 February to 31 October (2008-2009) and once weekly from 1 November through end of firearms season (6 December 2008 and 7 December 2009) to determine general location of deer and mortalities. I removed any 3-dimensional fixes with position dilution of precision values > 10 and 2-dimensional fixes with position dilution of precision values > 5 (Moen et al. 1997, Dussault et al. 2001, D'Eon and Delaparte 2005).

Prey Exposure and Hunter Effort

Predation risk-allocation hypothesis assumes that prey can discriminate between magnitude and temporal variation in risk; however, this may not be accurate and should be evaluated (Lima and Steury 2005). Prior research found 3 days of exposure to predators provided prey with an adequate assessment of magnitude and temporal variation in risk (Sih and McCarthy 2002, Laurila et al. 2004, Foam et al. 2005, Brown et al. 2006, Ferrari et al. 2009); however, this period may vary among species (Ferrari et al. 2009). To determine if deer can discriminate between changes in magnitude (i.e., risk levels) and temporal variation (i.e., diurnal and nocturnal periods) in human predation risk, I considered days 1-3 of the hunting season as initial exposure (i.e., 22-24 November 2008; 21-23 November 2009) followed by days 4-13 (i.e., prolonged exposure = 25, 28-30 November 2008; 24, 27-30 November 2009; 1-2, 4-7 December 2008; 1, 3-6 December 2009). Furthermore, hunting season is typically 16 days long; however, I did not permit hunting on 3 days each year (2008: 26-27 November, 3 December; 2009: 25-26 November, 2 December) resulting in a non-contiguous season.

Hunter effort provided a metric of general hunting pressure across the study area and throughout the hunting season. I required hunters to spend a minimum of 4 hours each day during a weekend (i.e., 2008: 22-23, 28-30 November, 6-7 December; 2009: 21-22, 27-29 November, 5-6 December) in their hunting compartment; however, I could only enforce specific densities on weekends. This resulted in variable levels of hunting pressure on the study area during the week. I calculated hunter effort (i.e., hours/hectare/day) by dividing the number of hunted hours within each treatment by treatment size for each day. Additionally, I calculated hunter effort within each treatment

by hunter exposure (i.e., initial and prolonged) to quantify effort during the hunting season.

Movement Behaviors and Space Use

I evaluated influence of risk levels (i.e., no risk, low-risk, and high-risk), temporal variation (i.e., diurnal and nocturnal), and exposure to risk (i.e., initial and prolonged) on deer movement patterns using two metrics (Webb et al. 2009, 2010). I used the Animal Movement tool within Hawth's Tools (Beyer 2004) in ArcGIS 9.3 (ESRI, Inc., Redlands, CA) to calculate step length (i.e., distance between successive points) and net displacement (i.e., distance between the first point in the data set and the current point). I calculated total hourly step length for each deer by date, exposure, risk level, and temporal period. I examined potential bias in movement distances by evaluating number of GPS fixes per hour (i.e., 1 to 8 fixes). This evaluation resulted in exclusion of hourly values with < 7 fixes/hour because movement distances were biased low (A. R. Little, personal observation). Using the total hourly step length (hereafter, movement rate), I calculated an average hourly movement rate by individual deer for each date, exposure, risk level, and temporal period.

I calculated tortuosity to describe path complexity or linearity and intensity of use of an area (Turchin 1998). Tortuosity values nearer to zero represent more linear movements, simpler movement trajectories, and reduced use of an area, while increasing values represent more complex movements and increased use of an area (Webb et al. 2011*a*). To estimate tortuosity of deer paths, I used the formula log (L/R^2), where L is step length and R is net displacement (Whittington et al. 2004). However, I chose to

model R^2 as opposed to R because R^2 typically increases linearly with path length (Turchin 1998, Whittington et al. 2004, Webb et al. 2011*a*). I calculated average hourly tortuosity for each deer by date, exposure, risk level, and temporal period, while excluding hours with < 7 fixes. Using the hourly tortuosity, I calculated an average value for each individual deer, date, exposure, risk level, and temporal period. I $\log_{10}$-transformed the ratio of L/R^2 to correct for heteroscedasticity and a right-skewed distribution of residuals across fitted values (Whittington et al. 2004).

White-tailed deer exhibit site fidelity to previously established ranges; however, human predation risk may cause deer to increase or decrease site fidelity. To address this question, I examined if the probability of use of hunted treatments (i.e., low- and high-risk) decreased following initial exposure (days 1-3) by calculating total number of re-locations that occurred across the study area and number of re-locations that occurred within the hunted treatments for each deer by day and exposure. Decreased use of hunted treatments would indicate that, despite strong site fidelity of adult male deer (Hellickson et al. 2008), hunters influenced distribution of deer as exposure increased.

Statistical Analysis

To test effects of risk levels (i.e., no, low, and high), temporal variation in risk (i.e., diurnal and nocturnal hours), and exposure to risk (i.e., initial and prolonged), I used a 3-way analysis of variance with repeated measures (PROC MIXED—SAS Institute Inc. 2003), with day as the repeated measure, a compound symmetry covariance structure, year as a random effect to account for unmeasured environmental variation and similarity of data within years, and deer identification as subject. I used the Kenward-Roger degrees

of freedom to account for unbalanced data, multiple random effects, and any model with correlated errors (Kenward and Rodger 1997, Littell et al. 2006). The assumption of normality was met.

I used generalized linear mixed models (GLMM; PROC GLIMMIX) and a logistic regression framework to calculate probability of adult male deer shifting use from hunted areas (i.e., low- and high-risk) to the non-hunted control area following initial exposure. I included year as a random effect to account for unmeasured environmental variation and similarity of data within year. Based on the hierarchical data structure, I set the subject equal to day nested within deer identification to account for correlation by day within individual animals. For the GLMM, I used a binomial distribution, logit-link function and a variance components covariance structure to model GPS count data. I used the Kenward-Roger degrees of freedom to account for unbalanced data, multiple random effects, and any model with correlated errors (Kenward and Rodger 1997, Littell et al. 2006). Because of the lack of research on this topic, I used $\alpha = 0.10$ for all statistical tests reduce the chance of Type II error (Tacha et al. 1982).

RESULTS

I deployed 52 collars (25 in 2008, 27 in 2009) on adult male deer during the study. However, I analyzed data on 19 collars in 2008 and 18 collars in 2009, with 7 deer analyzed in both years. Fifteen deer were not included due to illegal harvest (n = 8), legal harvest (n = 1), mechanical failures of the collar (n = 3), natural mortality (n = 1), deer-vehicle collision (n = 1), and dispersal from the study area (n = 1). One of the 8 illegally-harvested deer required development of an underwater antenna to retrieve the collar from

a pond (Webb et al. 2011*b*). I analyzed movement and tortuosity using 52,930 locations on the study area, including 23,360 from 2008 and 29,570 from 2009. GPS collars averaged 96.8% (SD = 9.8) fix success and a 3.7-meter (SD = 7.6) error.

Hunter Effort

Hunter effort averaged 0.03 hrs/ha/day in the low-risk treatment and 0.10 hrs/ha/day in the high-risk treatment during the study period. Hunter effort declined between initial and prolonged exposure in both treatments: low-risk declined 25% from 0.04 to 0.03 hrs/ha/day and high-risk declined 40% from 0.15 to 0.09 hrs/ha/day. However, hunters continued to provide a significant hunting threat during the prolonged exposure with 320 and 1,151 hunter hours spent afield in the low- and high-risk areas, respectively.

Movement Behaviors and Space Use

There was no three-way interaction of risk levels (i.e., no, low, and high), temporal variation in risk (i.e., diurnal and nocturnal hours), and exposure to risk (i.e., initial and prolonged) on movement rate (m/hr) and tortuosity. Therefore, I addressed my research questions by evaluating the two-way interactions between risk levels and exposure to risk (Table 2.1), risk levels and temporal variation in risk (Table 2.2), and exposure and temporal variation in risk (Table 2.3).

The levels of risk used during my study did not alter movement rates of adult, male deer (Tables 2.1 and 2.2). However, tortuosity in the high-risk treatment was 5-fold greater than no- and low-risk treatments (Tables 2.1 and 2.2).

Exposure to predation risk levels altered significantly deer movement behaviors (Table 2.1). Deer decreased movement rate by 24% and tortuosity by 59% following the initial 3-day exposure, regardless of risk levels. Moreover, deer maintained high site fidelity within hunted and un-hunted areas during prolonged exposure ($F_{1,390} = 1.30$; $P = 0.255$). Probability of use of hunted treatments declined from initial (72.9%) to prolonged exposure (67.9%) by 6.9%.

Predation risk levels and time of day did not influence movement rates (Table 2.2). However, tortuosity increased by 84% from diurnal to nocturnal hours across all risk levels (Table 2.2), but much of this response can be traced to the 6-fold greater level during initial exposure nocturnal hours (Table 2.3).

Movement rate and tortuosity varied inconsistently by time of day within initial and prolonged exposure periods (Table 2.3). Movement rate declined from initial to prolonged exposure by 17% diurnally and 31% nocturnally. However, diurnal movement was 13% greater than nocturnal movements only during the prolonged exposure period. Nocturnal path complexity was 76% less than diurnal path complexity but only during prolonged exposure.

DISCUSSION

My results indicate that deer recognized human predation risk by decreasing movements and increasing tortuosity with greater predator density while maintaining high site-fidelity during prolonged hunting exposure, which fully supports the predation risk-allocation hypothesis. However, the low-risk treatment was likely too low of a density to influence movement behaviors, which results in a density threshold between

low- and high-risk levels. Moreover, Lima and Bednekoff (1999) predicted that prey would increase activities and foraging during periods of safety (e.g., nocturnal hours) within risky environments; however, contrary to their hypothesis, movement rates and tortuosity declined even during safe periods, which may indicate deer maintaining a heightened level of vigilance. Overall, these results indicate that humans can alter movement behaviors of a large mammal during hunting season.

Despite a decline in movement behaviors among all risk levels, my results indicate that adult male deer were able to recognize the high-risk level to an extent, which was evident in significantly greater diel path complexity relative to no- and low-risk levels. Decreased movement rates and increased path complexity within the high-risk treatment indicates that deer were responding strongly to human predation risk by using smaller areas more intensely. Moreover, Webb et al. (2010) found male deer decreased diurnal movement behaviors to potentially avoid contact with hunters.

Movement behaviors in the no- and low-risk levels were more similar than high-risk throughout the study period. One hunter per 101 ha may be too low of a density to dramatically impact deer movement behaviors. Root et al. (1988) reported deer movements were greatest when average hunter effort was 0.45 hrs/ha/day, which is 15 times greater than the low-risk and 4.5 times greater than the high-risk on my study area. My results indicate that 1 hunter per 30 ha was significant enough to impact deer movement behaviors.

Predation risk often varies across space and time, so prey must gain information on current presence or absence of predators and respond adaptively to fluctuations in risk (Sih 1992). Three days of exposure to hunters provided adult male deer with an adequate

assessment of predation risk, which is represented by declines in movement rates and tortuosity (Sih and McCarthy 2002, Laurila et al. 2004, Foam et al. 2005, Brown et al. 2006, Ferrari et al. 2009). However, this decline in movement behaviors may be confounded by post-breeding season, which cannot be separated due to time of hunting season.

The predation risk-allocation hypothesis posits that prey should increase activities and foraging during periods of safety (e.g., nocturnal hours) within risky environments. However, contrary to that hypothesis, movement rates and tortuosity also significantly declined during periods of safety. Similar to my findings, Sih (1992) suggests that uncertainty in whether predators are currently present or absent may increase vigilance due to the lack of specific information on risk of predation. Deer were able to recognize the relative magnitude of risk, as suggested by Ferrrari et al. (2009), but were unable to fully recognize the temporal variation in risk following 3 days of exposure. Furthermore, my results were consistent with previous research that found no increase in activity during periods of safety within risky environments (Mirza et al. 2006). Previous studies testing the risk-allocation hypothesis have led to conflicting results regarding changes in behaviors due to temporal variation in risk levels (Hamilton and Heithaus 2001, Sih and McCarthy 2002, Van Buskirk et al. 2002, Pecor and Hazlett 2003, Mirza et al. 2006), which suggests that future studies need to focus on different lengths of exposure to risk levels to provide prey with an adequate assessment of temporal variation in risk.

The question still exists as to why deer decreased movement behaviors and space use during periods of safety in an otherwise risky environment. Predation risk-allocation hypothesis posits that animals would increase their activity during periods of safety to

search for forage (Lima and Bednekoff 1999). However, deer may have lacked complete recognition of when hunters vacated the field thus resulting in decreased movements during nocturnal hours (i.e., period of safety). Moreover, lack of recognition of when hunters vacated the field may have led to an increased level of vigilance (Hunter and Skinner 1998, Altendorf et al. 2001, Benhaiem et al. 2008). To address this issue in future research, I suggest extending the period of initial exposure to allow deer to clearly recognize periods of safety and risk.

My prediction that adult male deer would shift space use to non-hunted areas was not supported by my results. This minor change in treatment use supports previous studies that found adult male deer did not greatly alter use of hunted and non-hunted areas (Root et al. 1988, Webb et al. 2007, Hellickson et al. 2008, Karns 2008) but rather maintained normal home ranges. Male deer tend to select a home range that is large enough to provide all the essentials for life and reproduction, yet small enough that the deer can be familiar with the area, which has the potential to increase survival (Marchinton and Hirth 1984). Additionally, movements confined within home ranges may reduce mortality, stress, and energy expenditure (Webb et al. 2009) rather than making excursions outside of their normal home range and increasing risk of predation.

Although this study did demonstrate certain adjustments to immediate predation risk, adult male deer may have modified behaviors based on prior experiences with hunting pressure. Prey animals continually modify responses to predation risk, and much of this change can be attributed to their ability to learn (Brown and Chivers 2005). Hunting pressure on surrounding properties and within the study area may have caused a learned experience to avoid hunters. Although there was no hunting on the study area one

year prior, deer studied in this project had at least one year of possible hunter pressure experience as fawns and potentially at other ages on adjacent properties and during the first year of data collection. Thus, my study animals likely were not totally naïve to recreational hunting risk. Illegal harvest of 8 animals prior to legal firearms season indicates there also was risk outside of the legal firearms season. These prior experiences also may have attributed to the lack of predator density effect on movement rates. Predation risk is extremely variable throughout time with risk changes occurring year to year, season to season, day to day, and even moment to moment, which causes prey to fine tune predator avoidance to recent experiences (Brown and Chivers 2005).

Overall, this study provides evidence that humans affect deer movement behaviors at 1 hunter per 30 hectares, which supports the predation risk-allocation hypothesis. However, low-risk (1 hunter/101 ha) did not significantly influence movement behaviors, which suggests that a density threshold between low- and high-risk likely exists. This will need to be addressed with future research to determine where this threshold exists. Furthermore, research is needed to address if using longer exposure periods would lead to deer being able to fully recognize the temporal variation in risk. Decreased movements during nocturnal hours suggest that deer may have been maintaining a heightened level of vigilance due to a lack of recognition that hunters had vacated the field. Populations of animals living in disturbed environments may need to be monitored to determine if, and when, human activity influences population demographics or dynamics (Webb et al. 2011*c*). As urbanization and habitat fragmentation increases, and populations of large carnivores decrease across North America, researchers and land

managers must continue to monitor the effects of human activity on behavioral ecology of wildlife species.

ACKNOWLEDGEMENTS

This study was funded by the Samuel Roberts Noble Foundation and Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture. Samuel Roberts Noble Foundation provided the study site and recruited employees, family, and friends to participate in hunting the property. R. Stevens, D. Payne, and F. Motal provided technical and field assistance. This is Mississippi State University Forest and Wildlife Research Center publication number WF-XXX.

LITERATURE CITED

Altendorf, K. B., J. W. Laundre, C. A. Lopez-Gonzalez, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430-439.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611-618.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed May 1, 2009.

Brown, G. E., and D. P. Chivers. 2005. Learning as an adaptive response to predation. Pages 34-54 *in* P. Berbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, Inc., New York, New York, USA.

Brown, G. E., A. C. Rive, M. C. O. Ferrari, and D, P, Chivers, 2006. The dynamic nature of anti-predator behaviour: prey fish integrate threat-sensitive anti-predator responses within background levels of predation risk. Behavioral Ecology and Sociobiology 61:9-16.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143-164.

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

Dussault, C., R. Courtois, J.P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. Wildlife Society Bulletin 29:171-179.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Foam, P. E., R. S. Mirza, D. P. Chivers, and G. E. Brown. 2005. Juvenile convict cichlids (*Archocentrus nigrofasciatus*) allocate foraging and antipredator behaviour in response to temporal variation in predation risk. Behaviour 142:129-144.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1-16.

Gee, K. L., M. D. Porter, S. Demarais, F. C. Bryant, and G. Van Vreede. 1994. White-tailed deer: their foods and management in the Cross Timbers. Second edition. Samuel Roberts Noble Foundation Publication, Ardmore, Oklahoma, USA.

Gee, K. L., J. H. Holman, and S. Demarais. 1999. A man-power efficient drop-net system for capturing white-tailed deer. 22nd Annual Southeast Deer Study Group Meeting 22:31.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387-393.

Hamilton, I. M., and M. R. Heithaus. 2001. The effects of temporal variation in predation on antipredator behaviour: an empirical test using marine snails. Proceedings of the Royal Society of London, Series B 268:2585-2588.

Hellickson, M. W., T. A. Campbell, K. V. Miller, R. L. Marchinton, and C. A. DeYoung. 2008. Seasonal ranges and site fidelity of adult male white-tailed deer (*Odocoileus virginianus*) in southern Texas. Southwestern Naturalist 53:1-8.

Hunter, L. T. B., and J. D. Skinner. 1998. Vigilance behavior in African ungulates: the role of predation pressure. Behaviour 135:195-211.

Kammermeyer, K. E., and R. L. Marchinton. 1975. The dynamic aspects of deer populations utilizing a refuge. Pages 466–475 *in* W. A. Rogers,W.Wegener and L. E.Williams, Jr., editors. Proceedings of the 29th Annual Conference Southeast Association of Game and Fish Commissioners, St. Louis, Missouri, USA.

Karns, G. R. 2008. Impact of hunting pressure on adult male white-tailed deer behavior. Thesis, North Carolina State University, Raleigh, USA.

Kenward, M. G., and J. H. Roger. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53:983-997.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359-1364.

Kolter B. P., J. E. Gross, and W. A. Mitchell. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. Journal of Wildlife Management 58:299-307.

Kreeger, T. J. 1996. Handbook of Wildlife Chemical Immobilization. Veterinary Services. Wildlife Pharmaceuticals, Fort Collins, Colorado, USA.

Laurila, A., M. Jarvi-Laturi, S. Pakkasmaa, and J. Merila. 2004. Temporal variation in predation risk: stage-dependency, graded responses and fitness costs in tadpole antipredator defences. Oikos 107:90-99.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215-290.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and T. D. Steury. 2005. Perception of predation risk: the foundation of nonlethal predator-prey interactions. Pages 166-188 *in* P. Barbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS® for mixed models. Second edition. SAS Institute, Inc., Cary, North Carolina, USA.

Marchinton, R. L., and D. H. Hirth. 1984. Behavior. Pages 129-168 *in* L. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Miller, K. A., J. P. Garner, and J. A. Mench. 2006. Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. Animal Behaviour 71:1323-1334.

Mirza, R. S., A. Mathis, and D. P. Chivers. 2006. Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. Ethology 112:44-51.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.

Morrison, M. L., W. M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2010. Wildlife study design. Second edition. Springer Science, New York, New York, USA.

Pecor, K. W., and B. A. Hazlett. 2003. Frequency of encounter with risk and the tradeoff between pursuit and antipredator behaviors in crayfish: a test of the risk allocation hypothesis. Ethology 109:97-106.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Root, B. G., E. K. Fritzell, and N. F. Giessman. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin 16:145-151.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-216.

Sih, A. 1987. Direct and indirect impacts on aquatic communities. University Press of New England, Hanover, USA.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist 139:1052-1069.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437-443.

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

Tacha, T C., W. D. Wade, and K. P. Burnham. 1982. Use and interpretation of statistics in wildlife journals. Wildlife Society Bulletin 10:355-362.

Tarlow, E. M., and D. T. Blumstein. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. Applied Animal Behaviour Science 102:429-451.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59-73.

Van Buskirk, J., and K. L. Yurewicz. 1998. Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. Oikos 82:20-28.

Van Buskirk, J., C. Muller, A. Portmann, and M. Surbeck. 2002. A test of the risk allocation hypothesis: tadpole responses to temporal change in predation risk. Behavioral Ecology 13:526-530.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555-558.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210-1217.

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

Webb, S. L., M. R. Dzialak, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011*a*. Effects of human activity on space use and movement patterns of female elk. Wildlife Society Bulletin 35:261-269.

Webb, S. L. J. A. Gaskamp, K. L. Gee, S. Demarais, and A. R. Little. 2011*b*. Design of an underwater telemetry antenna for locating and retrieving submerged radiocollars. Wildlife Society Bulletin 35:101-104.

Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011*c*. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. Population Ecology 53:483-493.

Whittington, J., C. C. St. Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecology and Society 9:4. Available from: http://www.ecologyandsociety.org/vol9/iss1/art4.

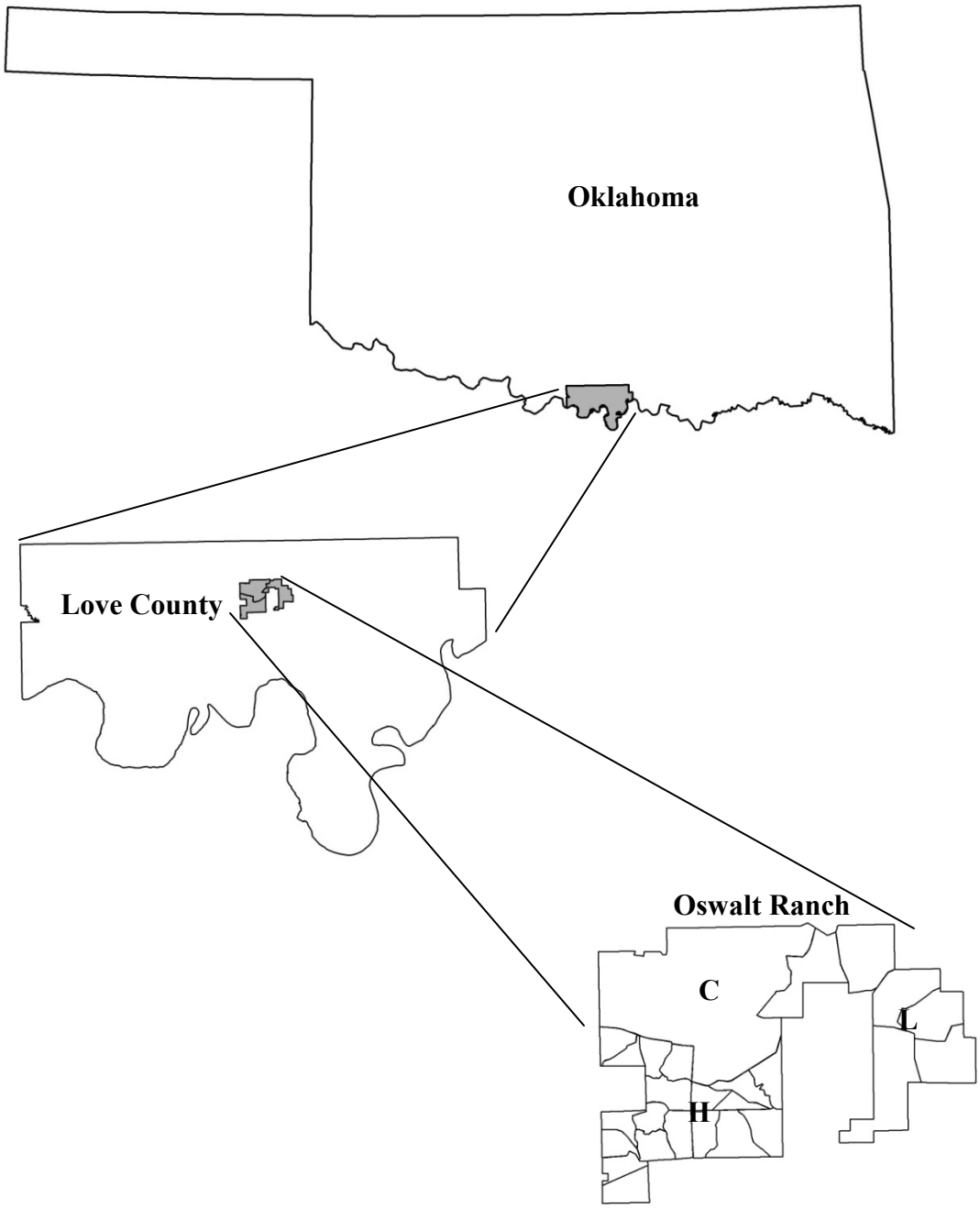

Figure 2.1. Samuel Roberts Noble Foundation Oswalt Ranch with denoted treatments control (C) = no hunters on 679 ha; low-risk (L) = 1 hunter/101 ha on 585 ha; and high-risk (H) = 1 hunter/30 ha on 583 ha) during 2008, located in Love County, Oklahoma, USA. Treatments were shifted clockwise during 2009
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Table 2.1. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; high-risk = 1 hunter/30 ha) and exposure to risk (initial = days 1-3 of season; prolonged = days 4-13 of season) on movement rate (m/hr) and tortuosity of adult, male white-tailed deer (≥ 2.5 years) in south-central Oklahoma during 2008-2009.

		Exposure[a]									*P*-value	
		Initial			Prolonged			Combined			Exposure	Interaction
	Risk Levels	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE		
Movement Rate[b]	Control	10	455.5	54.3	14	306.8	46.7	14	381.2	47.2		0.165
	Low	16	432.7	51.6	15	325.4	45.7	17	379.0	45.4		
	High	16	409.3	49.1	16	351.5	45.4	18	380.4	44.6		
	Combined	29	432.5	43.7	29	327.9	41.6				<0.001[c]	
	P-value								0.998			
Tortuosity[d]	Control	10	0.35	0.21	14	0.07	0.05	14	0.12A[e]	0.06		0.753
	Low	16	0.37	0.22	15	0.03	0.01	17	0.11A	0.05		
	High	16	0.77	0.36	16	0.61	0.33	18	0.57B	0.28		
	Combined	29	0.64	0.21	29	0.26	0.11				0.038	
	P-value								0.031			

[a]Exposure: Initial (22-24 November 2008, 21-23 November 2009); Prolonged (25 November-7 December 2008, 24 November-6 December 2009)
[b]Least square means presented
[c]Refer to interaction in Table 2.3
[d]Actual means presented (multiplied by 100 for display); *P*-values correspond to log transformed data
[e]Differences among combined treatment means are designated by different letters

Table 2.2. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; high-risk = 1 hunter/30 ha) and temporal variation in risk (diurnal = 0600-1800; nocturnal = 1800-0600) on movement rate (m/hr) and tortuosity of adult, male white-tailed deer (≥ 2.5 years) in south- central Oklahoma during 2008 - 2009.

		Temporal Variation in Risk									*P*-value	
		Diurnal			Nocturnal			Combined			Temporal Variation in Risk	Interaction
	Risk Levels	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE		
Movement Rate[a]	Control	11	387.0	51.1	14	375.3	50.1	14	381.2	47.2		0.880
	Low	16	380.4	49.0	16	377.7	48.1	17	379.0	45.4		
	High	18	393.2	47.1	16	367.5	47.2	18	380.4	44.6		
	Combined	30	386.9	42.7	30	373.5	42.6				0.495	
	P-value								0.998			
Tortuosity[b]	Control	11	0.13	0.11	14	0.12	0.07	14	0.12A[c]	0.06		0.506
	Low	16	0.07	0.03	16	0.18	0.11	17	0.11A	0.05		
	High	18	0.48	0.33	16	0.76	0.35	18	0.57B	0.28		
	Combined	30	0.25	0.11	30	0.46	0.18				0.007	
	P-value								0.031			

[a]Least square means presented
[b]Actual means presented (multiplied by 100 for display); *P*-values correspond to log transformed data
[c]Differences among combined treatment means are designated by different letter

Table 2.3 Effects of exposure (initial = days 1-3 of season; prolonged = days 4-13 of season) and temporal variation in risk (diurnal = 0600-1800; nocturnal = 1800-0600) on movement rate (m/hr) and tortuosity of adult, male white-tailed deer (≥ 2.5 years) in south-central Oklahoma during 2008 - 2009.

		Exposure[a]						*P*-value	
		Initial			Prolonged				
	Temporal Variation in Risk	n	$\bar{x}$	SE	n	$\bar{x}$	SE	Exposure	Interaction
Movement Rate[b]	Diurnal	29	422.4	47.0	29	351.4	42.9	0.013	0.087
	Nocturnal	29	442.7	46.7	29	304.4	42.7	<0.001	
	P-value		0.551			0.018			
Tortuosity[c]	Diurnal	29	0.18	0.10	29	0.28	0.14	0.595	0.004
	Nocturnal	29	1.11	0.37	29	0.27	0.15	<0.001	
	P-value		0.001			0.878			

[a]Exposure: Initial (22-24 November 2008, 21-23 November 2009); Prolonged (25 November-7 December 2008, 24 November-6 December 2009)
[b]Least square means presented
[c]Actual means presented (multiplied by 100 for display); *P*-values correspond to log transformed data

CHAPTER III

CHANGING RESOURCE USE PATTERNS OF WHITE-TAILED DEER IN THE PRESENCE OF HUMAN PREDATION RISK

ABSTRACT

Recreational hunting is the primary management tool for ungulate populations across North America; however, the potential for white-tailed deer (*Odocoileus virginianus*) to increase antipredator behaviors (e.g., altered resource selection) to avoid encounters with hunters has not been addressed within the context of the risk-allocation hypothesis. I evaluated resource selection of 37 adult (≥ 2.5 years) male deer at 3 risk levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha), 2 temporal periods of risk (diurnal = 6 a.m. - 6 p.m.; nocturnal = 6 p.m. - 6 a.m.), and 2 exposure periods (initial = days 1-3; prolonged = days 4-13) on a 1,861-ha study area in Oklahoma during the 2008 and 2009 rifle deer seasons. I used generalized linear mixed models under a logistic regression framework to model probability of deer resource use relative to magnitude and temporal variation in risk. Forested cover was the most important landscape variable, followed by mixed cover, elevation, and slope; distance to nearest road was least important. Diurnal use of forested cover increased during prolonged exposure among all treatments; however, deer in the high-density treatment increased probability of use of forested cover 1.7 times more than no- and low-risk.

Likewise, nocturnal use of mixed cover increased among all treatments, but deer in the high-density treatment increased probability of use of mixed cover 2.3 times more than no- and low-risk. Deer generally selected higher elevations, gentle slopes, and areas away from roads; however, these results varied among magnitude and temporal variation in risk. Collectively, these findings suggest that adult male deer alter resource selection in the presence of human predation risk by increasing use of security cover, higher elevations, gentle slopes, and by avoiding roads. These results support the predation risk-allocation hypothesis that prey respond to magnitude and temporal variation in risk by altering resource selection.

INTRODUCTION

Predation is a fundamental ecological and evolutionary process that can shape antipredator behaviors among prey species (Ydenberg and Dill 1986, Lima and Dill 1990, Hebblewhite et al. 2005, Mirza et al. 2006, Chalfoun and Martin 2009). Selective pressure has changed with elimination of large carnivores and replacement by human hunters (Ripple and Beschta 2004). In some instances, animals that are approached by humans likely respond similarly to those approached by natural predators (Frid and Dill 2002). Furthermore, predators can alter prey distribution and habitat selection through nonlethal behavioral effects (Lima and Dill 1990, Schmitz et al. 1997). However, little information exists on whether hunters cause deer to alter their resource selection to avoid risk of predation.

To avoid risk of predation, prey may choose different antipredator behavior modifications such as shifting their habitat use to safer locations (Ydenberg and Dill

1986, Lima and Dill 1990, Sih and McCarthy 2002, Chalfoun and Martin 2009). These behavioral modifications can allow prey to avoid immediate and possibly long term risk of predation, which subsequently leads to increased survivorship (Lima 1998). However, prey must learn to recognize risk of predation while balancing their need to meet minimum energy requirements (Lima and Bednekoff 1999, Brown and Chivers 2005).

Understanding importance of predation risk assessment is critical to wildlife management because predator avoidance can cause prey to have less time and energy to allocate towards other necessary activities such as foraging (Altendorf et al. 2001, Brown and Chivers 2005). However, to fully understand prey response to predation risk the magnitude and temporal variation in risk must be accounted for. Lima and Bednekoff (1999) recognized critical aspect in gaining an understanding in antipredator behaviors and proposed the predation risk-allocation hypothesis. Their hypothesis posits that prey living in safe environments with brief periods of risk should increase antipredator behaviors (e.g., decreased activity and foraging) during risky situations, whereas, prey living in risky environments with brief periods of safety should decrease antipredator behaviors (e.g., increased activity and foraging) during safe times. However, if risk levels stay elevated for an extended period of time, then prey are left with the choice of dying or increasing activity and foraging during risky times to meet energy requirements.

Ungulates respond to predation risk by increasing use of security cover, higher elevations, and areas away from roads (Kilgo et al. 1998, Mysterud and Østbye 1999, Lingle 2002, Ripple and Beschta 2004, Stankowich 2008). Such alterations in resource use can reduce predation (Bowyer et al. 1998, Mysterud and Østbye 1999, Creel et al. 2005, Dzialak et al. 2011). To survive, animals must learn to balance predation risk with

resource consumption because either choice will carry costs (Liley and Creel 2007), which supports the theory that prey will assess current predation risk levels and make behavioral adjustments to recreational hunters.

My research evaluated potential changes in resource selection of adult male deer due to human predation risk under the risk-allocation hypothesis. To examine resource selection under this hypothesis, I accounted for magnitude of risk by using multiple levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and temporal variation in risk diurnally (6 a.m. - 6 p.m.) when hunters were present and nocturnally (6 p.m. - 6 a.m.) when hunters were absent. Furthermore, I provided deer with 3 days of initial exposure (i.e., days 1-3 of season) to human predation risk followed by prolonged exposure (days 4-13 of season) to decrease uncertainty in magnitude and temporal variation in risk (Ferrari et al. 2009).

My research was designed to quantify how adult, male white-tailed deer perceive and respond to human predation risk during the hunting season. Based on the predation risk-allocation hypothesis, I hypothesized that deer would seek landscape features which distance or conceal them from hunters. Moreover, I hypothesized that deer would avoid detection by selecting greater vertical structure (i.e., mixed and forested areas), lower elevations, steeper slopes, and areas farther from roads while hunters were present (i.e., diurnal hours) during prolonged exposure. This hypothesis is based on hunters using areas that provide the greatest visual advantage to locate deer. Conversely, I hypothesized that deer would recognize when hunters vacated the field (i.e., nocturnal hours) and increase probability of use of areas with less vertical structure (i.e., grasslands), higher elevations, gentle slopes, and areas closer to roads during prolonged exposure. This

hypothesis is based on deer recognizing hunters have vacated the field and shifting their use to areas that may provide increased opportunities for forage. These hypotheses are based on the theory that prey will assess the current predation risk levels and make behavioral adjustments to recreational hunters.

STUDY AREA

I conducted this study on the 1,861 ha Samuel Roberts Noble Foundation Oswalt Ranch (NFOR) in Love County located in south-central Oklahoma (Figure 2.1). The NFOR is located in the Cross Timbers and Prairies ecoregion, and contains oaks (*Quercus* spp.), elms (*Ulmus* spp.), hickories (*Carya* spp), ashes (*Fraxinus* spp.), hackberries (*Celtis* spp.), osage orange (*Maclura pomifera),* bluestems (*Andropogon* spp.), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans)*, and numerous forbs (Gee et al. 1994). The NFOR is rurally located, with minimal road density (1.4 km/km^2) bounding and within the study area. Elevation ranges from 233 m to 300 m and slope ranges from 0 degrees to 41 degrees across the study area (U.S. Department of Agriculture-National Cartography and Geospatial Center). During 2008 and 2009 study periods, rainfall ranged from 0 to 0.41 cm and average temperature was 6.9° C (Burneyville, OK; Oklahoma Mesonet). During the study, NFOR was a non-operational ranch with no cattle grazing or prescribed fire management. Lease hunting ($\bar{x}$ = 5 hunters) ended after the 2006 hunting season to minimize effects of previous hunting exposure on study animals. Coyotes (*Canis latrans*) occurred on the study area.

I divided the NFOR into no risk (control; 679 ha), low-risk (1 hunter/101 ha; 585 ha), and high-risk (1 hunter/30 ha; 583ha) treatments based on existing landscape

features, property boundaries, and fencing, with the goal of producing 3 areas of similar size and vegetative composition (Figure 2.1). Percentage cover of forest, mixed forest/grassland, and grassland was similar within the control, low-risk, and high-risk treatments. I divided the low- and high-risk treatments into smaller hunter compartments comparable to the desired risk levels, which distributed hunter effort uniformly within each treatment. I randomly relocated treatments during the second year, which shifted treatments clockwise to create temporal replication (Morrison et al. 2010). Hunting effort varied on surrounding properties each year, ranging from none to high-risk.

METHODS

Capture and Handling

I captured 52 adult male white-tailed deer (≥ 1.5 years of age) during winters of 2008 (n = 25) and 2009 (n = 27) using drop nets (Gee et al. 1999). I aged deer according to tooth replacement and wear (Severinghaus 1949), but due to variations in wear patterns (Gee et al. 2002), I classified them as ≥ 1.5 years at capture, and all deer were ≥ 2.5 years of age by the study period. I sedated deer with an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Kreeger 1996). Prior to release, I weighed, ear-tagged, and affixed each deer with a GPS collar (ATS G2000 Remote-Release GPS, Advanced Telemetry Systems, Isanti, MN). The Institutional Animal Care and Use Committee at Mississippi State University approved all capture, handling, and marking techniques (Protocol 07-034).

I programmed GPS collars to acquire location estimates every 8 minutes from 7 November through the end of the study (6 December 2008 and 7 December 2009). Each

location included Universal Transverse Mercator coordinates, date, time, fix status, position dilution of precision, and horizontal dilution of position. Mortality sensors indicated inactivity after 8 hours. I monitored deer once monthly from 1 February to 31 October (2008-2009) and once weekly from 1 November through end of firearms season (6 December 2008 and 7 December 2009) to determine general location of deer and mortalities. I removed 3-dimensional fixes with position dilution of precision values > 10 and 2-dimensional fixes with position dilution of precision values > 5 (Moen et al. 1997, Dussault et al. 2001, D'Eon and Delaparte 2005).

Prey Exposure and Hunter Effort

Predation risk-allocation hypothesis assumes that prey have perfect knowledge of the risk regime; however, this may not be accurate and should be evaluated (Lima and Steury 2005). Prior research found 3 days of exposure to predators provided prey with an adequate assessment of magnitude and temporal variation in risk (Sih and McCarthy 2002, Laurila et al. 2004, Foam et al. 2005, Brown et al. 2006, Ferrari et al. 2009); however, this period may vary among species (Ferrari et al. 2009). To determine if deer can discriminate between changes in magnitude (i.e., risk levels) and temporal variation (i.e., diurnal and nocturnal periods) in human predation risk, I considered days 1-3 of the hunting season as initial exposure (i.e., 22-24 November 2008; 21-23 November 2009) followed by days 4-13 (i.e., prolonged exposure = 25, 28-30 November 2008; 24, 27-30 November 2009; 1-2, 4-7 December 2008; 1, 3-6 December 2009). Additionally, the hunting season is typically 16 days long; however, I did not permit hunting on 3 days

each year (2008: 26-27 November, 3 December; 2009: 25-26 November, 2 December) resulting in a non-contiguous season.

Hunter effort provided a metric of general hunting pressure across the study area and throughout the hunting season. I required hunters to spend a minimum of 4 hours each day during a weekend (i.e., 2008: 22-23, 28-30 November, 6-7 December; 2009: 21-22, 27-29 November, 5-6 December) in their hunting compartment; however, I could only enforce specific densities on weekends. This resulted in variable levels of hunting pressure on the study area during the week. I calculated hunter effort (i.e., hours/hectare/day) by dividing number of hunted hours within each treatment by treatment size for each day. Additionally, I calculated hunter effort within each treatment by hunter exposure (i.e., initial and prolonged) to quantify effort during the hunting season.

Landscape Classification

To evaluate landscape features that may influence resource selection of deer, I developed a vegetation type map. Using 2009 growing-season National Agriculture Imagery Program aerial imagery, I re-sampled a 1-meter resolution grid into a 17-meter resolution grid using ERDAS Imagine 9.3 (ERDAS, Inc, Atlanta, GA) software. I reclassified to 17-meter resolution based on fractal analyses (Webb et al. 2009) because that was the smallest patch size perceived by deer and because most location errors were ≤ 3.7 meters.

Based on spatial scale and vegetative structure of the study area, I used 3 vegetative cover types: forest, mixed forest/grassland (hereafter, mixed), and grassland. I

classified forested areas as having greater than 70% closed canopy cover, grasslands as having greater than 70% open areas, and mixed forest/grassland areas as having less than 70% of both closed canopy (i.e., forest) and open areas (i.e., grassland). I measured visual obstruction at 90 stratified, randomly placed vegetation plots (i.e., 30 in each cover type) using a 1.8-m Nudds density board (Nudds 1977) separated into 6 equal 0.3-m sections. The board was viewed from a distance of 10-m in each cardinal direction by a standing observer from a standardized height of 1.5-m and obstruction of each section was estimated in 20% increments. Classification of vegetation types corresponded to visual obstruction, which provided a range of percentage of obstruction for each vegetation type. I analyzed estimates using the mid-point of each range at the estimated coverage yielding maximum obstruction of 90%. I used a general linear model to test for differences in percentage visual obstruction. I compared means among forest, mixed, and grassland habitat types in PROC GLM (SAS Institute Inc. 2003).

I performed a supervised classification based on spectral signatures of known forest, mixed, and grassland areas. I calculated a zonal majority and majority fraction based on the 1-m imagery to classify each 17-m pixel into either forest, mixed, or grassland vegetative types (Lillesand et al. 2004). These functions compute the most commonly occurring value in each zone (17-m cell) and the fraction of the total zone that is occupied by the majority class. I masked roads, non-vegetated areas, and water before performing the supervised classification on the vegetation areas to prevent misclassifying these areas as a vegetation type. To evaluate accuracy of the supervised classification, I compared the re-classified image to 90 stratified, randomly placed vegetation plots (i.e., 30 in each cover type).

I obtained a 10-m resolution DEM from the U.S. Department of Agriculture-National Cartography and Geospatial Center (2009) and calculated elevation and degree of slope using Spatial Analyst in ArcGIS 9.3. I extracted values for each deer GPS location with the vegetation type (i.e., mixed = 1, forest = 2, and grassland = 3), elevation, and slope map layers using Intersect to Point within Hawth's Tools (Beyer 2004). I delineated roads (i.e., dirt, stone, and paved) bounding and within the study area that hunters used to travel to their hunting compartments. These roadways received greatest traffic during early morning and evening hours when hunters were entering and leaving the field, respectively. Using ArcGIS 9.3, I spatially joined all deer GPS locations to the nearest roadway.

Model Development and Analysis

I addressed my hypotheses using a resource selection function approach (Manly et al. 2002), which required the generation of random locations within the study area boundary equal to number of deer locations to assess nonrandom resource selection. I used Sampling Tools within Hawth's Tools to generate an equal number of random points within the study area boundary similar to a Design II analysis (Johnson 1980). I assigned vegetative cover (i.e., forest, mixed, and grassland), elevation, slope, and distance to nearest roads to all random points.

I used generalized linear mixed models (GLMM; PROC GLIMMIX) and a logistic regression framework to determine what factors influenced resource selection of adult male deer. Habitat selection was analyzed as a binomial response variable (1 = actual deer location; 0 = random location), which yields values proportional to the

probability of use of a resource unit (Boyce et al. 2002). I included random effects for year and deer identification to account for unmeasured environmental variation, similarity of data within year, and correlation within individual animals (Gillies et al. 2006). For the GLMM, I used a binary distribution, logit-link function, and a variance components covariance structure for random effects. Logistic regression is a simplistic approach to analyzing the probability of resource selection and is used widely for other statistical analyses in biology (Manly et al. 2002). Moreover, logistic functions have the desirable property of restricting values of w*(x) to the range of 0 to 1 (Manly et al. 2002).

I standardized all group-specific marginal beta coefficient estimates (SCE) to examine relative importance of variables among risk levels and time periods (Hamilton 1992). Furthermore, all forested and mixed security cover coefficient estimates are relative to grassland areas because prior research showed deer decreased use of open areas during hunting season (Kilgo et al. 1998). However, use of grassland areas can still be inferred by examining if forested and mixed security cover coefficient estimates are positive (i.e., decreased probability of use of grassland areas) or negative (i.e., increased probability of use of grassland areas). I used the SCE to calculate simple effect sizes (SES) to show differences from initial to prolonged exposure within risk levels. Lastly, I ranked the absolute value of each SCE from largest to smallest to assess relative importance of each landscape variable.

RESULTS

I deployed 52 collars (25 in 2008, 27 in 2009) on adult male deer during the study. However, I analyzed data on 19 collars in 2008 and 18 collars in 2009, with 7 deer

analyzed in both years. Fifteen deer were not included due to illegal harvest (n = 8), legal harvest (n = 1), mechanical failures of the collar (n = 3), natural mortality (n = 1), deer-vehicle collision (n = 1), and dispersal from the study area (n = 1). One of the 8 illegally harvested deer required development of an underwater antenna to retrieve the collar from a pond (Webb et al. 2011*a*). I analyzed resource selection using 52,790 actual deer locations (2008: 23,246; 2009: 29,544) and an equal number of random locations on the study area. GPS collars averaged 96.8% (SD = 9.8) fix success and a 3.7-meter (SD = 7.6) error.

Hunter Effort

Hunter effort averaged 0.03 hrs/ha/day in the low-risk treatment and 0.10 hrs/ha/day in the high-risk treatment during the study period. Hunter effort declined between initial and prolonged exposure in both treatments: low-risk declined 25% from 0.04 to 0.03 hrs/ha/day and high-risk declined 40% from 0.15 to 0.09 hrs/ha/day. However, hunters continued to provide a significant hunting threat during the prolonged exposure with 320 and 1,151 hunter hours spent afield in the low- and high-risk areas, respectively.

Resource Selection

Visual obstruction differed among the 3 vegetation types ($F_{2,87} = 150.35$, $P < 0.001$). Visual obstruction increased from grasslands ($\bar{x}$ =18.5, SE =1.3) to mixed ($\bar{x}$ =59.5, SE = 2.3) to forested ($\bar{x}$ = 68.0, SE = 2.7) areas, supporting the separation of forest, mixed, and grassland areas. Furthermore, using these vegetation plots (i.e., 30 in each cover type), I correctly classified forested (83.3%), mixed (82.8%), and grassland

(81.5%) areas. Overall classification accuracy and kappa statistics were 86.1% and 0.83, respectively.

Based on standardized coefficient estimate rankings, forested cover was the most important landscape variable, followed by mixed cover, elevation, and slope; distance to nearest road was least important (Table 3.1-3.2). Selection for forest (92% of cases, positive estimates = 11, negative estimates = 1) and mixed cover (100% of cases, positive estimates = 12) was consistently positive across risk levels and time periods during prolonged exposure; however, selection for elevation (58% of cases, positive estimates = 7, negative estimates = 5), slope (92% of cases, positives estimates = 1, negative estimates = 11), and distance to nearest road (58% of cases, positive estimates = 7, negative estimates = 5) was variable within risk levels and time periods (Tables 3.1-3.2; Figures 3.1-3.12). Furthermore, forest and mixed vegetation types were ≥ 1.5 times more important than the other variables, so I only considered these 2 variables when evaluating magnitude, temporal variation, and exposure to risk. Moreover, forested and mixed vegetation types provide security cover from hunters, which should be associated with behavioral responses to varying risk levels.

Diurnal and nocturnal probability of use of forested cover increased among all treatments following initial exposure (SES $\bar{x}$ = 40.9, range = 21.4 to 72.3, Tables 3.1-3.2). Diurnal probability of use of forested cover in the high density treatment increased by 2.5 times, whereas nocturnal probability of use of forested cover doubled in the high-risk level from initial to prolonged exposure (Tables 3.1-3.2). Moreover, deer in the high-risk level increased the probability of use of forested cover 1.7 times greater than the no- and low-risk levels during diurnal, prolonged exposure (Tables 3.1-3.2).

Diurnal and nocturnal probability of use of mixed cover increased among all treatments following initial exposure (SES $\bar{x}$ = 25.5, range = 10.5 to 38.5, Tables 3.1-3.2). Furthermore, deer in the high-risk level increased the probability of use of mixed cover by 1.4 times greater than the no- and low-risk levels (Table 3.1). This pattern remained strong for nocturnal periods with an increase in probability of use of mixed cover by 2.3 times greater than the no- and low-risk levels (Table 3.2).

In addition to the findings on security cover selection, there were also other findings that indicated an avoidance of human predators. Probability of use of higher elevations increased in the high-risk level during diurnal and nocturnal periods following initial exposure (Tables 3.1-3.2; Figures 3.1-3.4). Use of areas farther from roads increased among all treatments during diurnal exposure while deer in the low- and high-risk levels moved closer to roads during nocturnal periods (Tables 3.1-3.2; Figures 3.9-3.12).

DISCUSSION

My results indicate that deer recognized human predation risk by seeking landscape features that distanced or concealed them from recreational hunters, which supports the predation risk-allocation hypothesis. However, deer maintained use of security cover during nocturnal hours with increasing predator density but to a lesser extent than diurnal hours, which suggests that 3 days of exposure to human predation risk was not long enough to fully recognize when hunters vacated the field. Nevertheless, my results indicate that humans can alter resource selection of white-tailed deer during hunting season.

As hypothesized, adult male deer increased probability of use of forested and mixed security cover with increasing predator density during diurnal periods and continued to use the security cover during nocturnal periods, but to a lesser extent. This response is similar to previous studies which found that ungulates shifted their use of open to forested areas to avoid predation during hunting season (Swenson 1982, Morgantini and Hudson 1985, Kilgo et al. 1998). Moreover, greater use of security cover in the high-risk level may indicate the need to find refuge areas where hunters were not currently present. By locating these areas, deer may have felt more secure from approaching predators which led to a reduction in vulnerability to harvest (Swenson 1982, Nelson and Woolf 1987, Kufeld et al. 1988, Kilgo et al. 1998, Mysterud and Ostbye 1999). Furthermore, deer are well adapted to their surroundings and know how to maximize use of escape cover (Dasmann and Taber 1956, Van Etten et al. 1965, Pilcher and Wampler 1981).

Magnitude and temporal variation in risk strongly influence antipredator decision-making; however, prey must gain information on the current presence or absence of predators to respond in the proper manner (Sih 1992, Lima and Bednekoff 1999, Ferrari et al. 2009). Three days of exposure to hunters provided adult male deer with an adequate assessment of predation risk, which is represented by the increase in use of security cover (Sih and McCarthy 2002, Laurila et al. 2004, Foam et al. 2005, Brown et al. 2006, Ferrari et al. 2009). However, deer among all treatment levels increased probability of use of security cover following 3 days of exposure to risk levels, which suggests that risk perception may be scale dependent because deer were unable to fully recognize when hunters entered or exited a risk level. Furthermore, increasing the exposure period would

likely provide deer with a better assessment of the magnitude and temporal variation in risk. Ferrari et al. (2009) found that longer initial exposure periods had a greater likelihood of detecting behavioral modifications among prey.

Lack of distinction between periods of risk and safety led deer to maintain use of security cover during nocturnal hours, but to a lesser extent. Deer appear to be unable to fully recognize when hunters vacate the field, which suggests that deer were maintaining a heightened level of vigilance. These findings were further supported by previous research suggesting that prey may be unable to fully recognize when predators vacate an area (Sih 1992). Furthermore, ungulates respond to predation risk by displaying greater levels of vigilance due to the possibility of an attack (Hunter and Skinner 1998, Altendorf et al. 2001, Benhaiem et al. 2008). Moreover, these changes may carry potential costs to survival and fitness and need to be addressed with future research.

Although security cover was the most important landscape feature used by deer to avoid risk of predation, there were other notable trends related to topographic and anthropogenic features (e.g., roads). Adult male deer generally selected higher elevations, gentle slopes, and areas away from roads. Despite these trends, these 3 landscape features were much less important in affecting antipredator behaviors in my study. However, animals tend to respond to predation risk in different ways based on physical adaptations to the environment. For example, caribou (*Rangifer tarandus*) and mule deer (*Odocoileus hemionus*) increased their use of higher elevations to avoid risk of predation (Bergerud and Page 1987, Lingle 2002, Kittle et al. 2008). In the face of predation risk, steeper slopes can offer a form of security from pursuing predators (Main and Coblentz 1990, Kotler et al. 1994, Lingle 2002), especially species well adapted to these environments.

Last, cervids tend to avoid roads because of increased human activity (Lyon 1979, Kilgo et al. 1998, Dzialak et al. 2011, Webb et al. 2011*b*).

Given the general trends across ungulate species in the presence of risk, white-tailed deer have adapted their own behavioral strategies to avoid predators (including humans). Therefore, I offer several explanations as to why adult, male white-tailed deer may not have shown an obvious propensity for certain landscape features. First, the range of elevational change across the study area was minimal; thus deer had limited choices. Moreover, hunters were likely present at varying elevations, which also left deer with few avoidance options. For these reasons, deer showed variable selection of elevation during the study.

White-tailed deer have adapted their antipredator behaviors to avoid predation risk on gentle terrain compared to other ungulates that use steeper slopes to avoid predation (Main and Coblentz 1990, Lingle 2002, Farmer et al. 2006). Subsequently, this adaptation likely led deer to increase their probability of use of gentle slopes. Moreover, hunters likely used gentle slopes due to ease of access; thus deer required other landscape features to avoid detection by hunters. This led to increased selection for security cover thereby decreasing the importance of other landscape features.

Roads are important anthropogenic features that provide hunters with access to remote areas (Forman and Alexander 1998). However, roads can act as a source of human intrusion into an environment and if ungulates perceive them as a threat they will likely respond negatively and use areas away from roads (Lyon 1979, Kilgo et al. 1998, Cole et al. 2004, Dzialak et al. 2011, Webb et al. 2011*b*). These studies support my findings that deer increased probability of use of areas away from roads when hunters

were present (i.e., diurnal hours). Conversely, deer in the low- and high-risk levels decreased probability of use of areas away from roads when hunters were absent (i.e., nocturnal hours). Roads on the study areas were not paved, but occasionally maintained, which may have provided enough disturbance along road sides to increase preferred forage resources (e.g., cool season forbs) for deer to use during nocturnal hours in the low- and high-risk levels. Despite these findings, roads were the least important variable among all landscape features, which also may be influenced by the minimal road density on the study area.

Despite increased antipredator behaviors (e.g., greater use of security cover); adult male deer may have modified their behaviors based on prior experiences with hunting pressure. Prey animals continually gain information on predation threats through visual, chemical, and social cues that enable them to learn how to avoid predation (Brown and Chivers 2005, Cronin 2005). Hunting pressure on properties surrounding and on the study area may have caused a learned experience to avoid hunters. Although there was no hunting on the study area one year prior, deer studied in this project had at least one year of possible hunter pressure experience as fawns and potentially at other ages on adjacent properties and during the first year of data collection. Thus, my study animals likely were not totally naïve to recreational hunting risk. Illegal harvest of 8 animals prior to legal firearms season indicates there also was risk outside of the legal firearms season. These learned experiences also may have attributed to the lack of predator density effect on movement rates. Predation risk is extremely variable throughout time with risk changes occurring year to year, season to season, day to day, and even moment to moment, which

causes prey to fine tune their predator avoidance to recent experiences (Brown and Chivers 2005).

Overall, this study provides evidence that adult male deer responded to human predation risk by altering resource selection of different landscape features to avoid human predation, which supports the predation risk-allocation hypothesis. Additional research is needed to address whether using longer exposure periods would lead to deer being able to fully recognize temporal variation in risk. Furthermore, my results indicate that deer were unable to fully recognize temporal variation in risk, which led them to maintain a greater use of landscape features that distanced or concealed them from recreational hunters.

ACKNOWLEDGEMENTS

This study was funded by the Samuel Roberts Noble Foundation and Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture. Samuel Roberts Noble Foundation provided the study site and recruited employees, family, and friends to participate in hunting the property. R. Stevens, D. Payne, and F. Motal provided technical and field assistance. This is Mississippi State University Forest and Wildlife Research Center publication number WF-XXX.

LITERATURE CITED

Altendorf, K. B., J. W. Laundre, C. A. Lopez-Gonzalez, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430-439.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611-618.

Bergerud, A.T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65: 1597-1606.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed May 1, 2009.

Bowyer, R. T., J. G. Kie, and V. van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415-425.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.

Brown, G. E., and D. P. Chivers. 2005. Learning as an adaptive response to predation. Pages 34-54 *in* P. Berbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, Inc., New York, New York, USA.

Brown, G. E., A. C. Rive, M. C. O. Ferrari, and D, P, Chivers, 2006. The dynamic nature of anti-predator behaviour: prey fish integrate threat-sensitive anti-predator responses within background levels of predation risk. Behavioral Ecology and Sociobiology 61:9-16.

Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497-503.

Cole, E.K., M.D. Pope, and R. G. Anthony. 2004. Influence of road management on diurnal habitat use of Roosevelt elk. Northwest Science 78:313-321.

Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 12:3387-3397.

Cronin, T. W. 2005. The visual ecology of predator-prey interactions. Pages 105-138 *in* P. Berbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, Inc., New York, New York, USA.

Dasmann, R. F., and R. D. Taber. 1965. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143-164.

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

Dzialak M.R., S.M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE 6: e14597.

Dussault, C., R. Courtois, J.P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. Wildlife Society Bulletin 29:171-179.

Farmer, C. J., D. K. Person, and R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. Journal of Wildlife Management 70:1403-1415.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Foam, P. E., R. S. Mirza, D. P. Chivers, and G. E. Brown. 2005. Juvenile convict cichlids (*Archocentrus nigrofasciatus*) allocate foraging and antipredator behaviour in response to temporal variation in predation risk. Behaviour 142:129-144.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1-16.

Gee, K. L., M. D. Porter, S. Demarais, F. C. Bryant, and G. Van Vreede. 1994. White-tailed deer: their foods and management in the Cross Timbers. Second edition. Samuel Roberts Noble Foundation Publication, Ardmore, Oklahoma, USA.

Gee, K. L., J. H. Holman, and S. Demarais. 1999. A man-power efficient drop-net system for capturing white-tailed deer. 22nd Annual Southeast Deer Study Group Meeting 22:31.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387-393.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898.

Hamilton, L. C. 1992. Regression with graphics: a second course in applied statistics. Brooks and Cole, Pacific Grove, California.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos 111:101-111.

Hunter, L. T. B., and J. D. Skinner. 1998. Vigilance behavior in African ungulates: the role of predation pressure. Behaviour 135:195-211.

Johnson, D. H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359-1364.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157:163-175.

Kolter B. P., J. E. Gross, and W. A. Mitchell. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. Journal of Wildlife Management 58:299-307.

Kreeger, T. J. 1996. Handbook of Wildlife Chemical Immobilization. Veterinary Services. Wildlife Pharmaceuticals, Fort Collins, Colorado, USA.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1988. Influence of hunting on movements of female mule deer. Journal of Wildlife Management 41:70-72.

Laurila, A., M. Jarvi-Laturi, S. Pakkasmaa, and J. Merila. 2004. Temporal variation in predation risk: stage-dependency, graded responses and fitness costs in tadpole antipredator defences. Oikos 107:90-99.

Liley, S., and S. Creel. 2007. What best explains vigilance in elk: characteristics of prey, predators, or the environment? Behavioral Ecology 19:245-254.

Lillesand, T. M., R. W. Kiefer, and J. W. Chipman. 2004. Remote sensing and image interpretation. Fifth edition. John Wiley and Sons, Inc., New York, New York, USA.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215-290.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and T. D. Steury. 2005. Perception of predation risk: the foundation of nonlethal predator-prey interactions. Pages 166-188 in P. Barbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83:2037-2048.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 77:658-660.

Main, M. B., and B. E. Coblentz. 1990. Sexual segregation among ungulates: a critique. Wildlife Society Bulletin 18:204-210.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Press, New York, New York, USA.

Mirza, R. S., A. Mathis, and D. P. Chivers. 2006. Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. Ethology 112:44-51.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.

Morgantini, L. E., and R. J. Hudson. 1985. Changes in diets of wapiti during a hunting season. Journal of Range Management 38:77-79.

Morrison, M. L., W. M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2010. Wildlife study design. Springer Science, New York, USA.

Mysterud, A., and E. Østbye 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385-394.

Nelson, T. A., and A. Woolf. 1987. Mortality of white-tailed deer fawns in southern Illinois. Journal of Wildlife Management 51:326-329.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113-117.

Pilcher, B. K., and G. E. Wampler. 1981. Hunting season movements of white-tailed deer on Fort Sill Military Reservation, Oklahoma. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 35:142-148.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78: 1388-1399.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-216.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist 139:1052-1069.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437-443.

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

Swenson, J.E., 1982. Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana.Wildlife Society Bulletin 10:115-120.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59-73.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210-1217.

Webb, S. L., J. A. Gaskamp, K. L. Gee, S. Demarais, and A. R. Little. 2011*a*. Design of underwater telemetry antenna for locating and retrieving submerged radiocollars. Wildlife Society Bulletin 35:101-104.

Webb, S. L., M. R. Dzialak, R. G. Osborn, S. M. Harju, J. J. Wondzell, L. D. Hayden-Wing, and J. B. Winstead. 2011*b*. Using pellet groups to assess response of elk and deer to roads and energy development. Wildlife Biology in Practice 1:32-40.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advanced Study Behaviour 16:229-249.

Table 3.1. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; high-risk = 1 hunter/30 ha) and exposure to risk (initial = days 1-3 of season; prolonged = days 4-13 of season) on probability of use of security cover, elevation (m), slope (°), and distance to road (m) during diurnal hours (0600 – 1800) by adult, male white-tailed deer (≥ 2.5 years) in south-central Oklahoma during 2008- 2009.

		Exposure[a]										
		Initial					Prolong					
		Raw		Standardized[b]			Raw		Standardized			
Variable	Risk Levels	β	SE	β	SE	Rank[c]	β	SE	β	SE	Rank	SES[d]
Forest[e]	Control	1.271	0.115	39.370	3.568	2	1.448	0.063	78.746	3.447	2	39.376
	Low	0.826	0.113	25.988	3.555	7	1.299	0.065	71.774	3.594	3	45.786
	High	1.285	0.088	48.277	3.319	1	1.994	0.060	120.560	3.630	1	72.283
Mixed	Control	1.034	0.106	31.558	3.250	3	1.207	0.058	64.744	3.133	5	32.619
	Low	0.891	0.113	26.078	3.300	6	1.018	0.065	49.935	3.206	6	23.857
	High	0.809	0.090	27.058	3.016	4	1.234	0.061	65.562	3.236	4	38.504
Elevation	Control	-0.018	0.003	-19.018	3.413	8	0.003	0.002	4.933	3.175	13	23.951
	Low	-0.006	0.003	-5.600	3.184	15	-0.017	0.002	-27.690	3.053	8	-22.090
	High	-0.024	0.003	-26.722	2.963	5	0.003	0.002	5.070	2.979	12	31.792
Slope	Control	-0.043	0.011	-11.640	3.068	10	-0.024	0.006	-11.269	2.934	11	0.371
	Low	0.046	0.010	14.501	3.256	9	-0.005	0.006	-2.630	2.967	15	-17.131
	High	-0.026	0.008	-8.797	2.779	12	-0.035	0.006	-17.368	2.819	9	-8.571
Distance to Road	Control	0.001	0.000	8.107	3.050	13	0.002	0.000	36.104	3.092	7	27.997
	Low	-0.001	0.000	-7.442	3.137	14	0.000	0.000	4.512	2.997	14	11.954
	High	0.001	0.000	9.910	2.691	11	0.001	0.000	12.676	2.905	10	2.766

[a]Exposure: Initial (22-24 November 2008, 21-23 November 2009); Prolong (25 November – 7 December 2008, 24 November – 6 December 2009)
[b]Standardized coefficient estimates
[c]Rank: Hierarchical numbering system of greatest to least important probability estimate based on absolute values
[d]SES: Simple effect size
[e]Forest and mixed security cover coefficient estimates are relative to grasslands.

Table 3.2. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; high-risk = 1 hunter/30 ha) and exposure to risk (initial = days 1-3 of season; prolonged = days 4-13 of season) on probability of use of security cover, elevation (m), slope (°), and distance to road (m) during nocturnal hours (1800 – 0600) by adult, male white-tailed deer (≥ 2.5 years) in south-central Oklahoma during 2008- 2009.

		Exposure[a]										
		Initial					Prolong					
		Raw		Standardized[b]			Raw		Standardized			
Variable	Risk Levels	β	SE	β	SE	Rank[c]	β	SE	β	SE	Rank	SES[d]
Forest[e]	Control	0.183	0.121	4.836	3.206	14	0.846	0.065	41.066	3.158	3	36.230
	Low	-0.395	0.113	-10.749	3.064	8	0.380	0.064	19.543	3.289	10	30.292
	High	0.613	0.092	20.640	3.092	1	0.757	0.058	42.080	3.215	2	21.440
Mixed	Control	0.290	0.110	7.977	3.033	11	0.475	0.058	23.356	2.829	7	15.379
	Low	0.357	0.109	9.788	2.989	10	0.428	0.062	20.328	2.945	9	10.540
	High	0.169	0.089	5.175	2.714	13	0.719	0.058	37.343	3.023	5	32.168
Elevation	Control	-0.011	0.003	-10.510	3.190	9	0.018	0.002	29.830	2.897	6	40.340
	Low	0.006	0.003	5.441	3.052	12	0.013	0.002	20.773	2.824	9	15.332
	High	0.013	0.003	14.919	2.867	5	0.030	0.002	57.134	2.971	1	42.215
Slope	Control	-0.062	0.012	-15.580	2.882	4	-0.096	0.007	-40.152	2.869	4	-24.572
	Low	-0.063	0.012	-15.764	2.994	3	-0.018	0.006	-8.216	2.935	13	7.548
	High	-0.039	0.009	-11.706	2.613	7	-0.014	0.005	-7.475	2.752	14	4.231
Distance to Road	Control	0.000	0.000	4.253	2.859	15	0.001	0.000	10.317	2.808	12	6.064
	Low	-0.002	0.000	-20.118	2.815	2	-0.000	0.000	-6.832	2.770	15	13.286
	High	-0.001	0.000	-13.917	2.659	6	-0.001	0.000	-18.466	2.921	11	-4.549

[a]Exposure: Initial (22-24 November 2008, 21-23 November 2009); Prolong (25 November – 7 December 2008, 24 November – 6 December 2009)
[b]Standardized coefficient estimates
[c]Rank: Hierarchical numbering system of greatest to least important probability estimate based on absolute values
[d]SES: Simple effect size
[e]Forest and mixed security cover coefficient estimates are relative to grasslands.

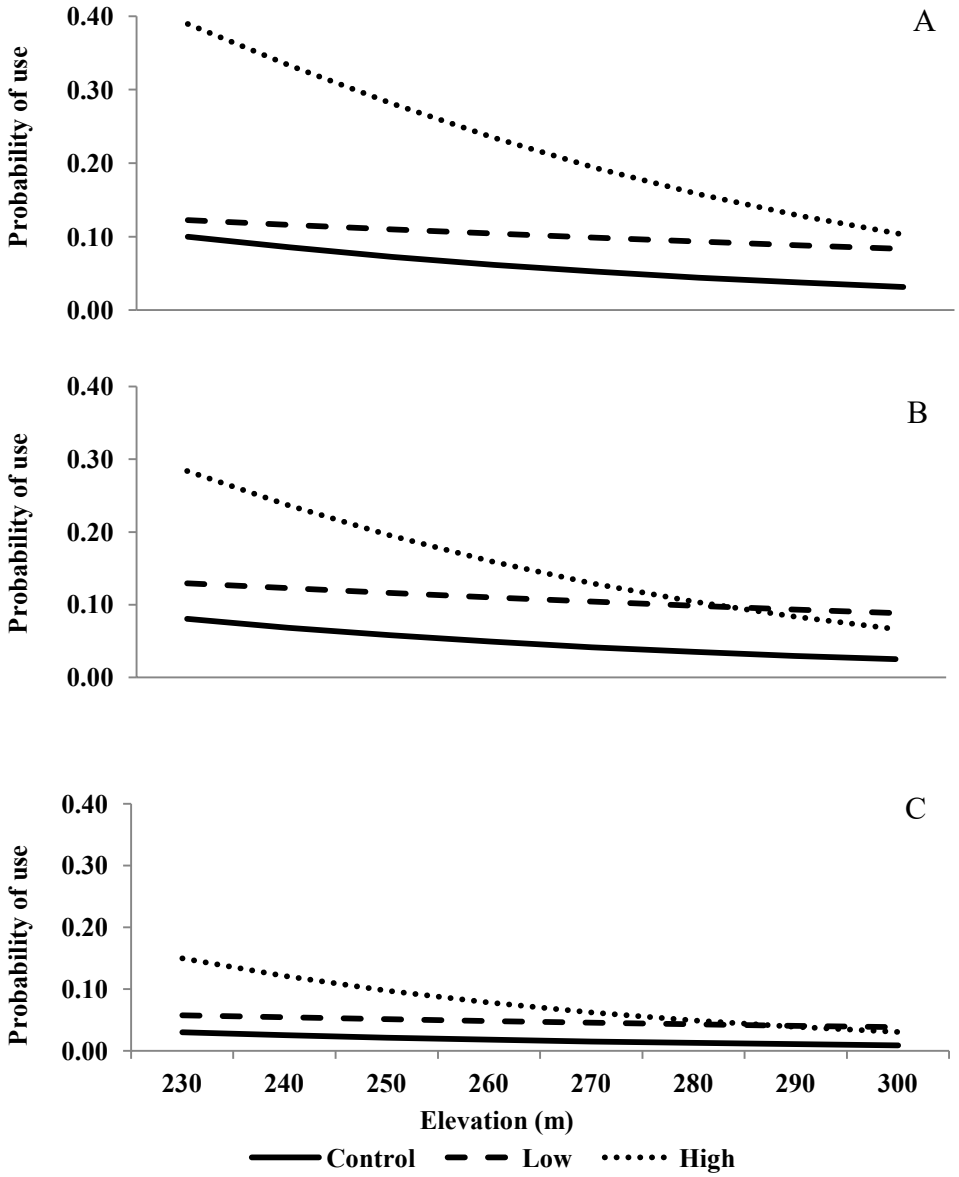

Figure 3.1. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of lower elevations during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

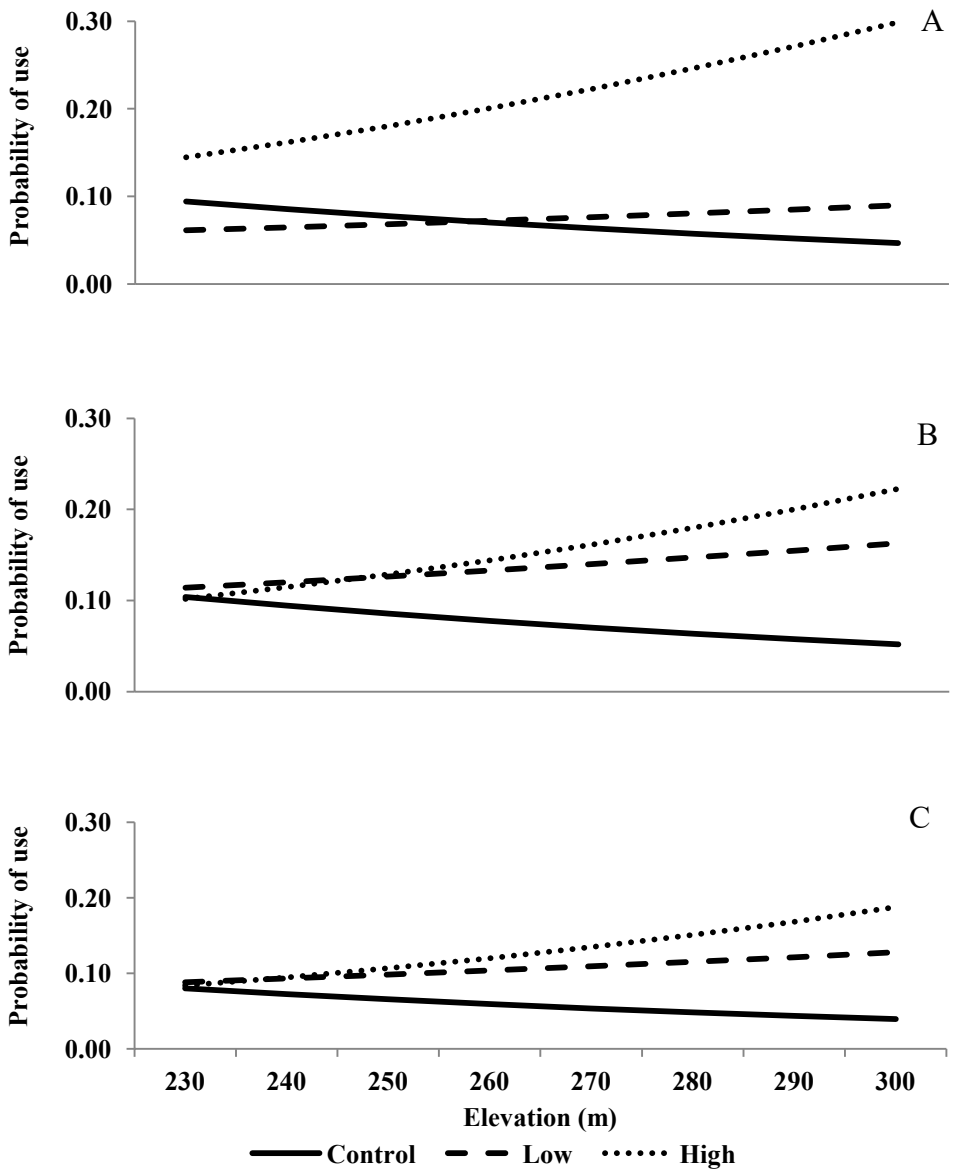

Figure 3.2. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of higher elevations during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

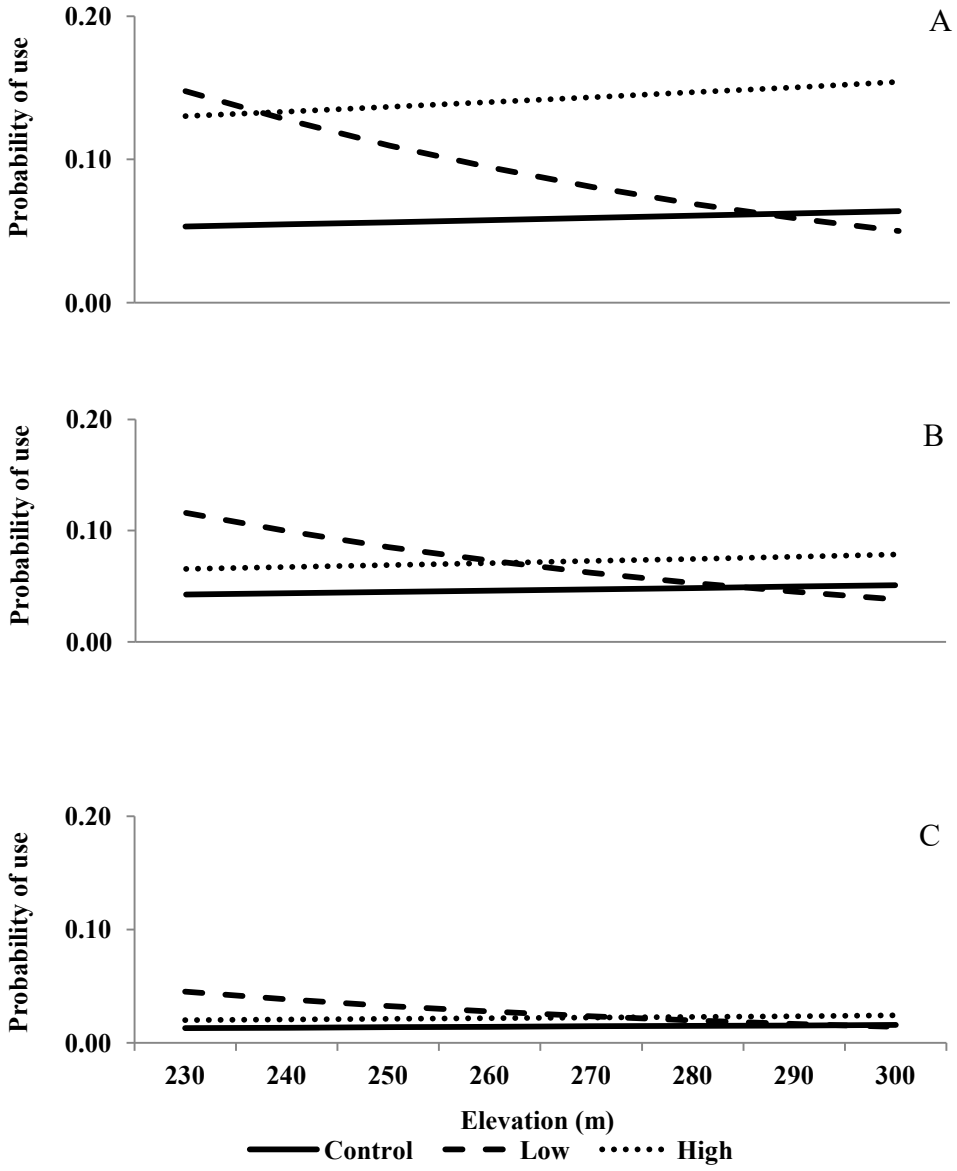

Figure 3.3. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of lower elevations during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

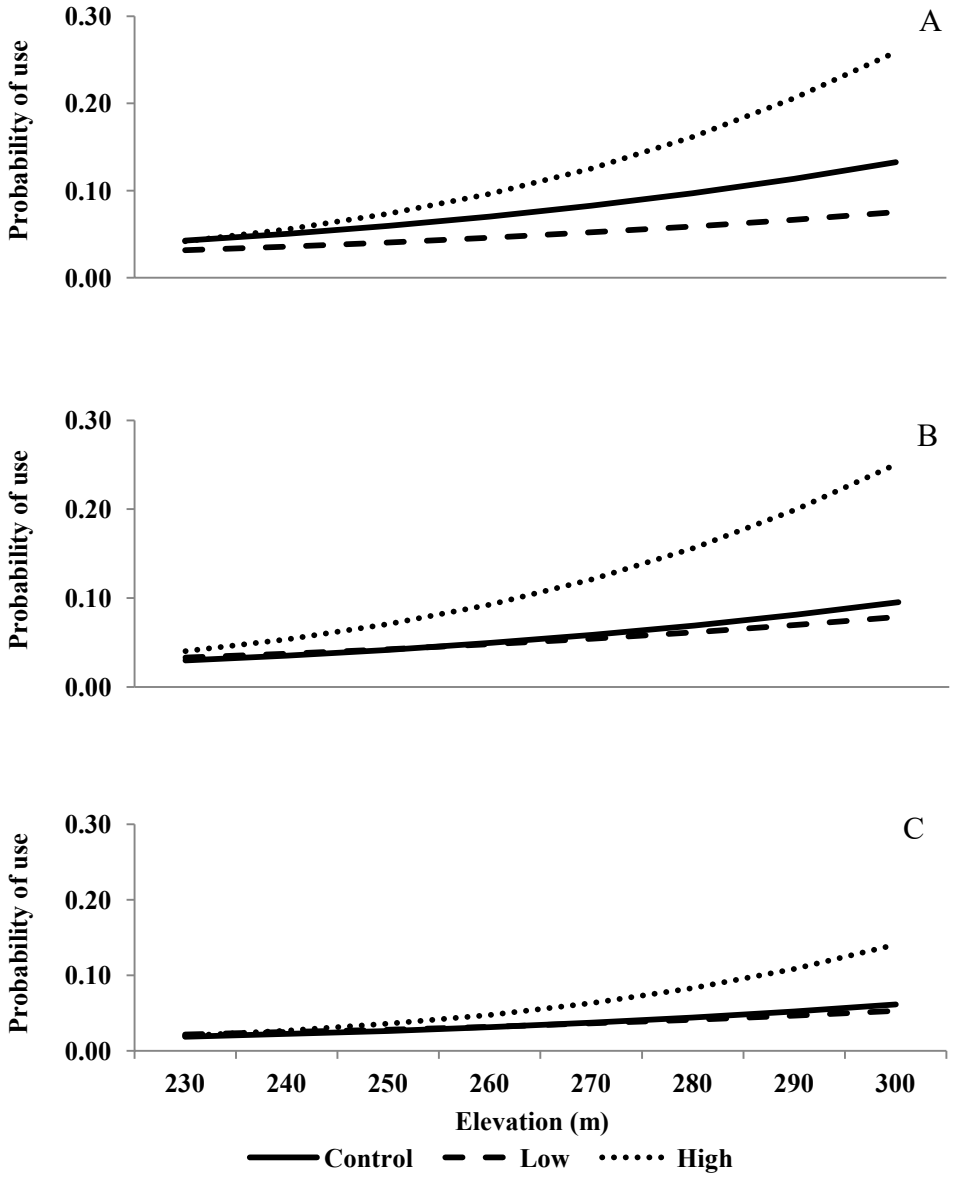

Figure 3.4. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of higher elevations during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

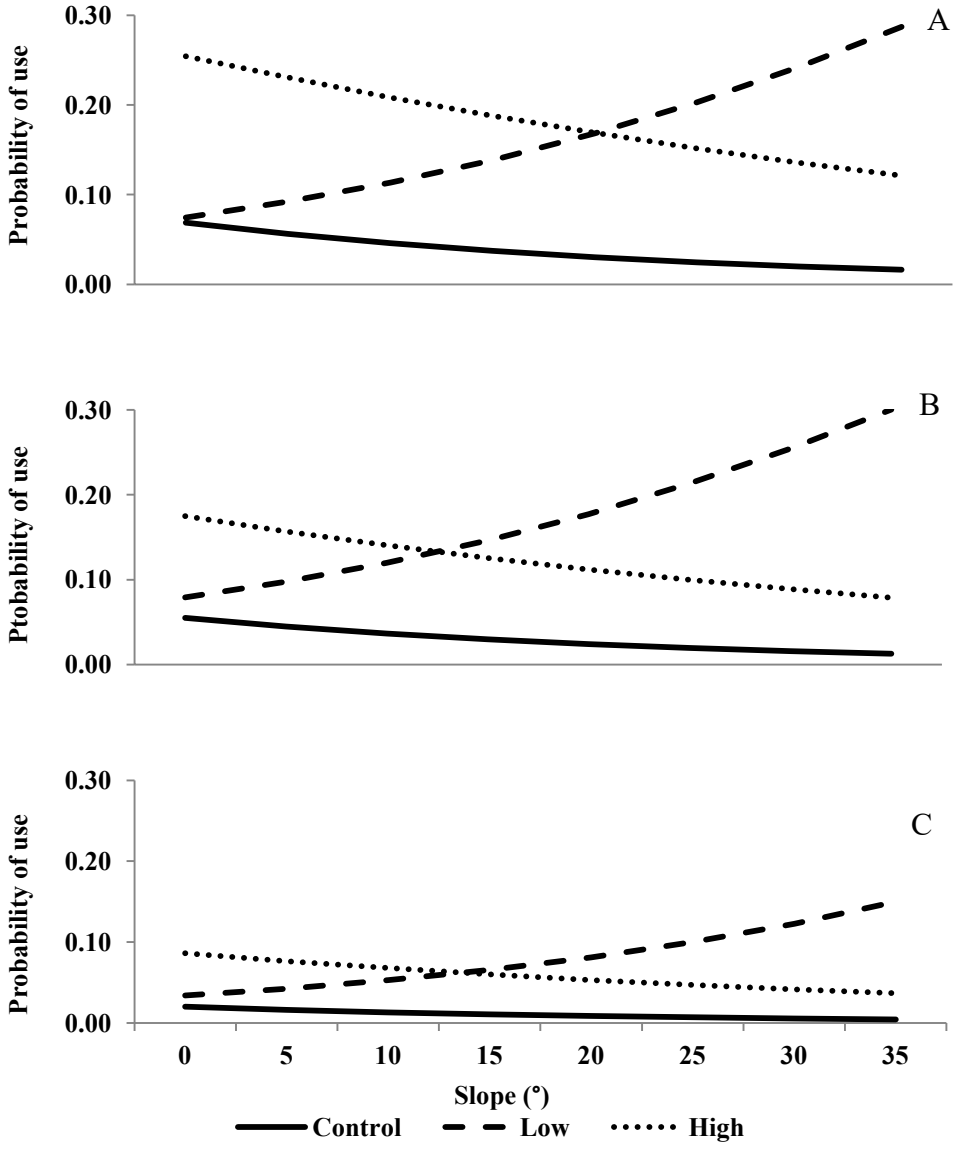

Figure 3.5. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of steeper slopes during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

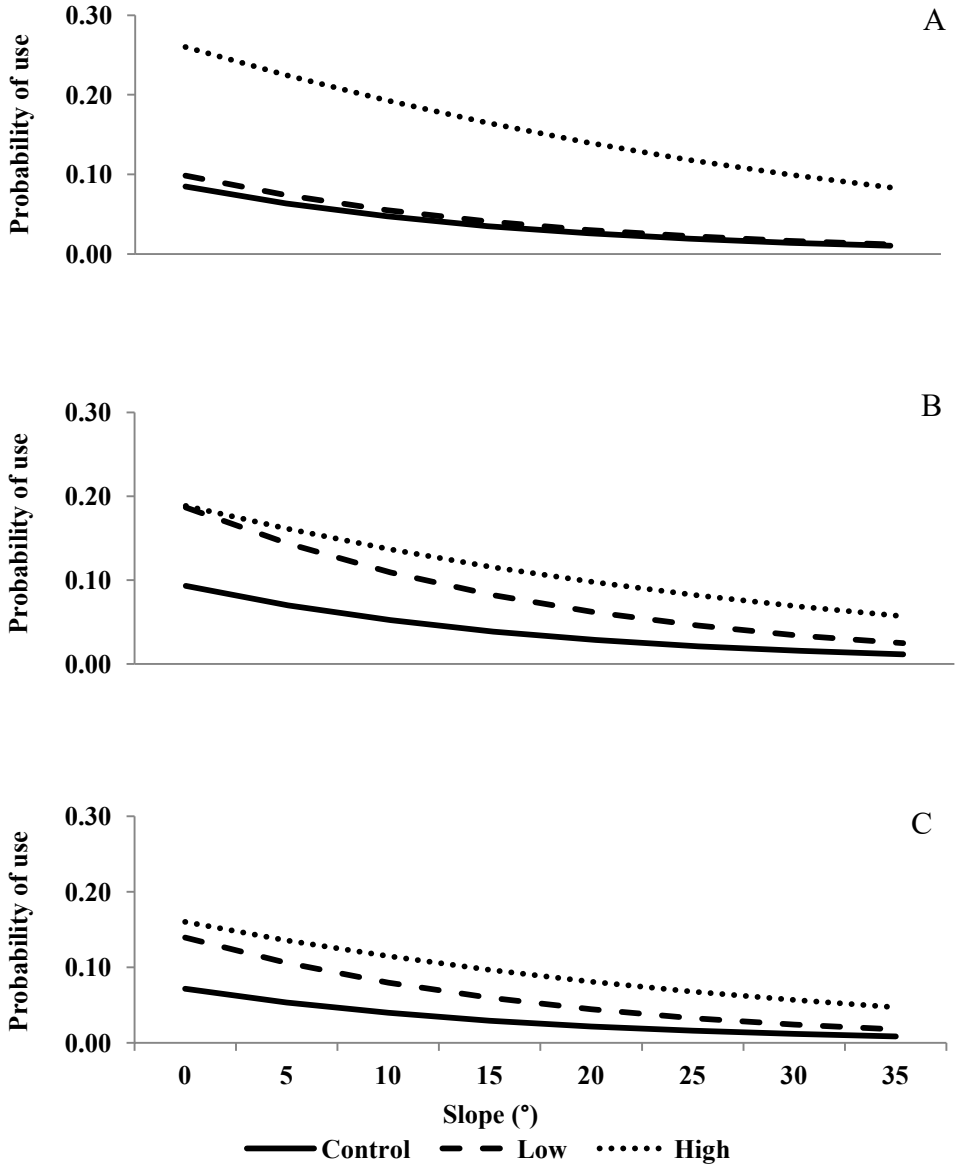

Figure 3.6. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of lower slopes during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

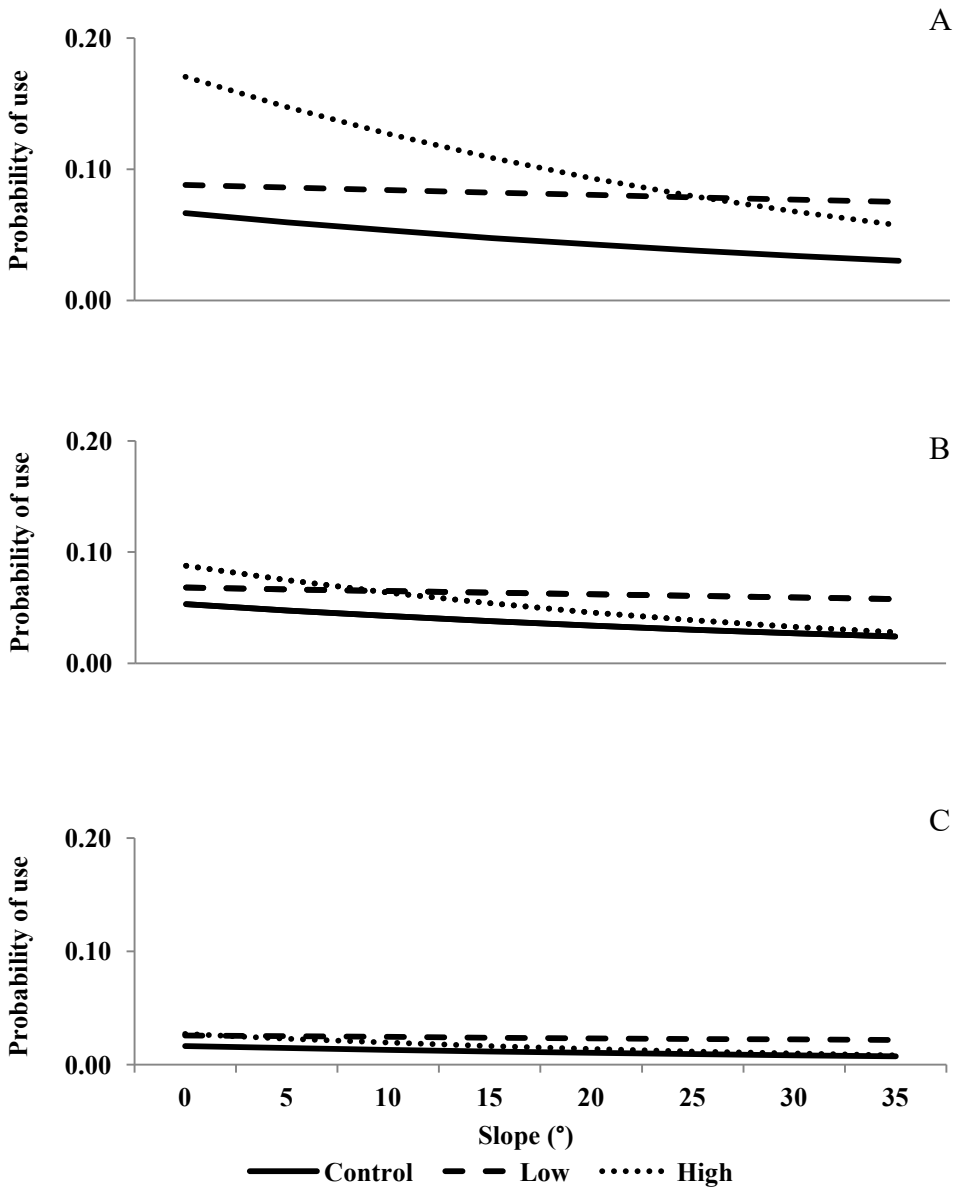

Figure 3.7. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of steeper slopes during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

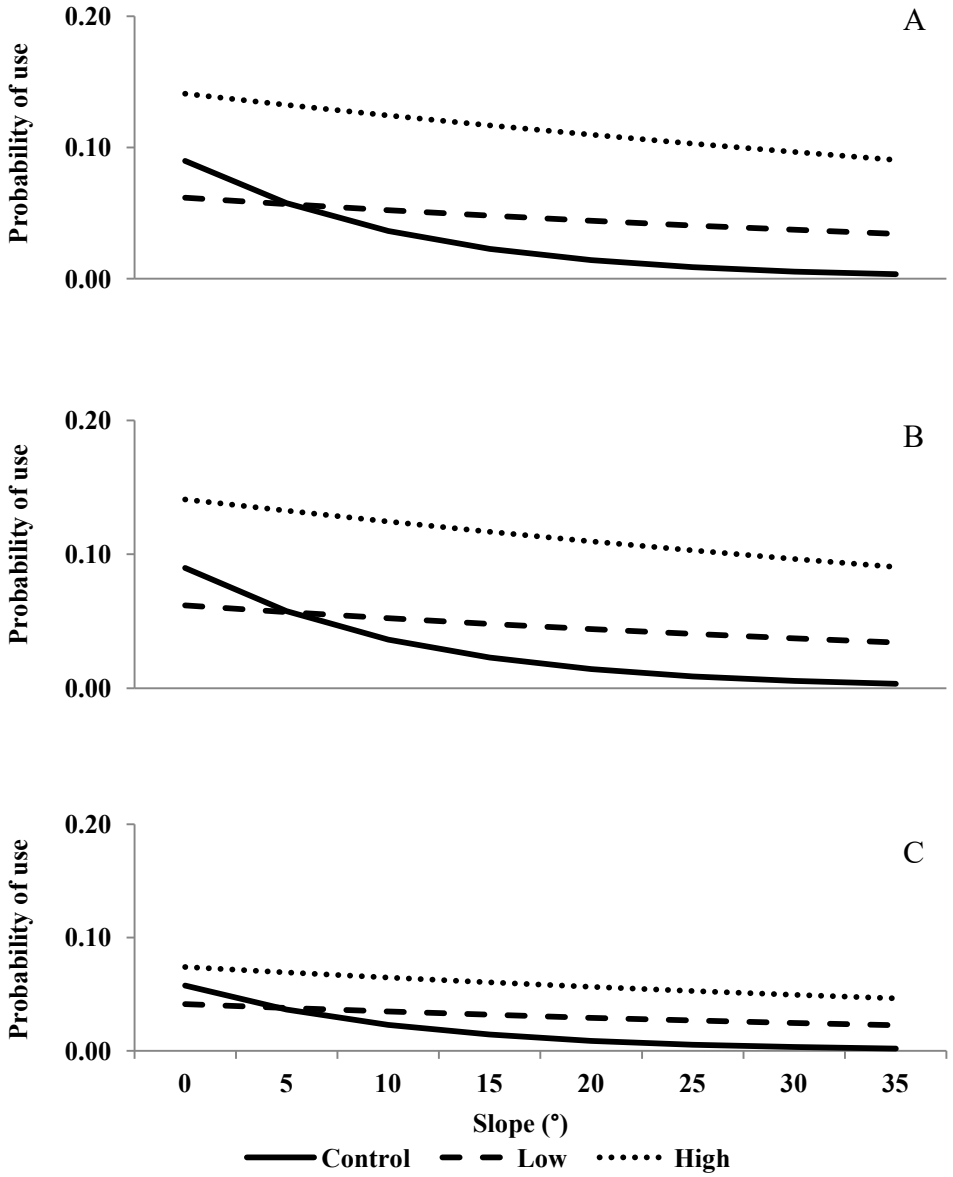

Figure 3.8. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of lower slopes during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

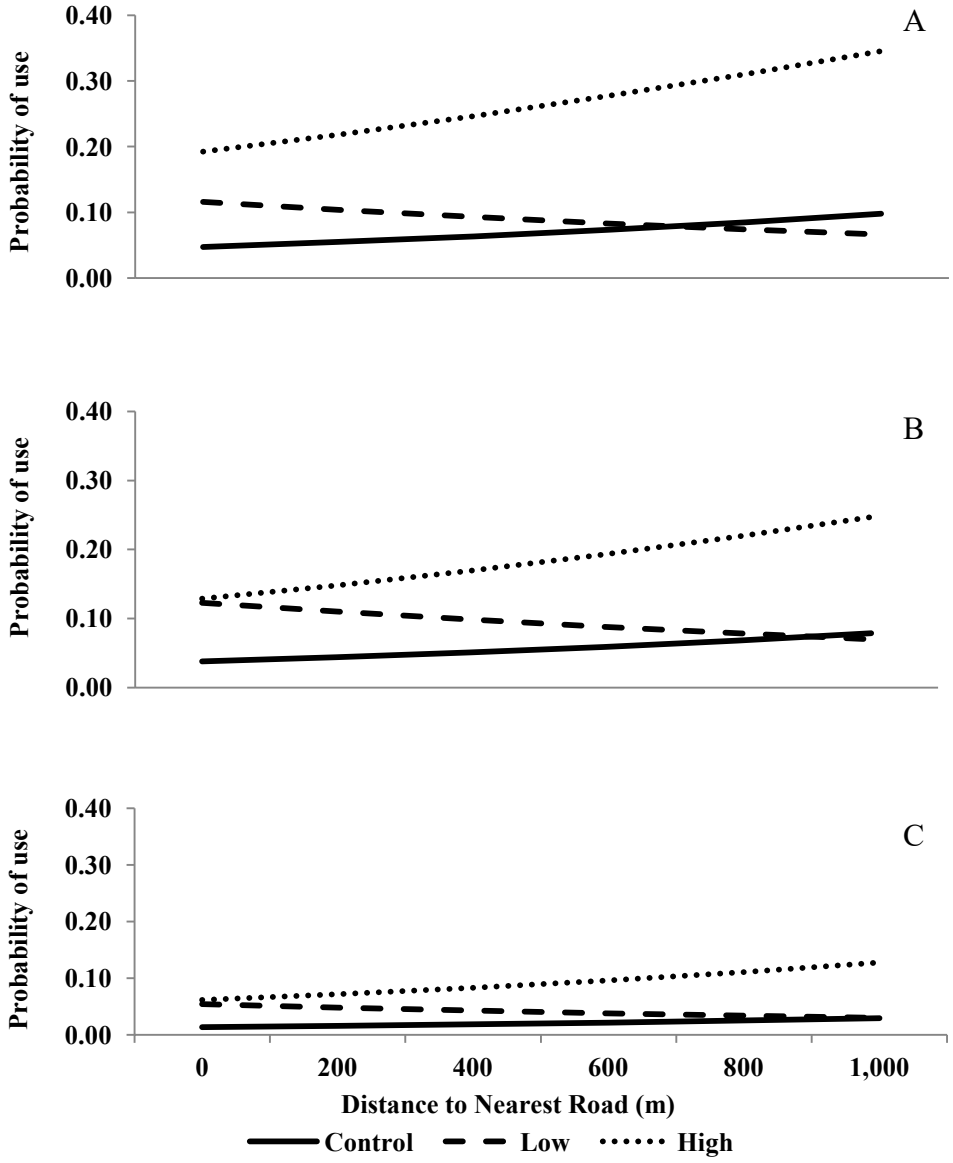

Figure 3.9. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of areas farther from roads during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

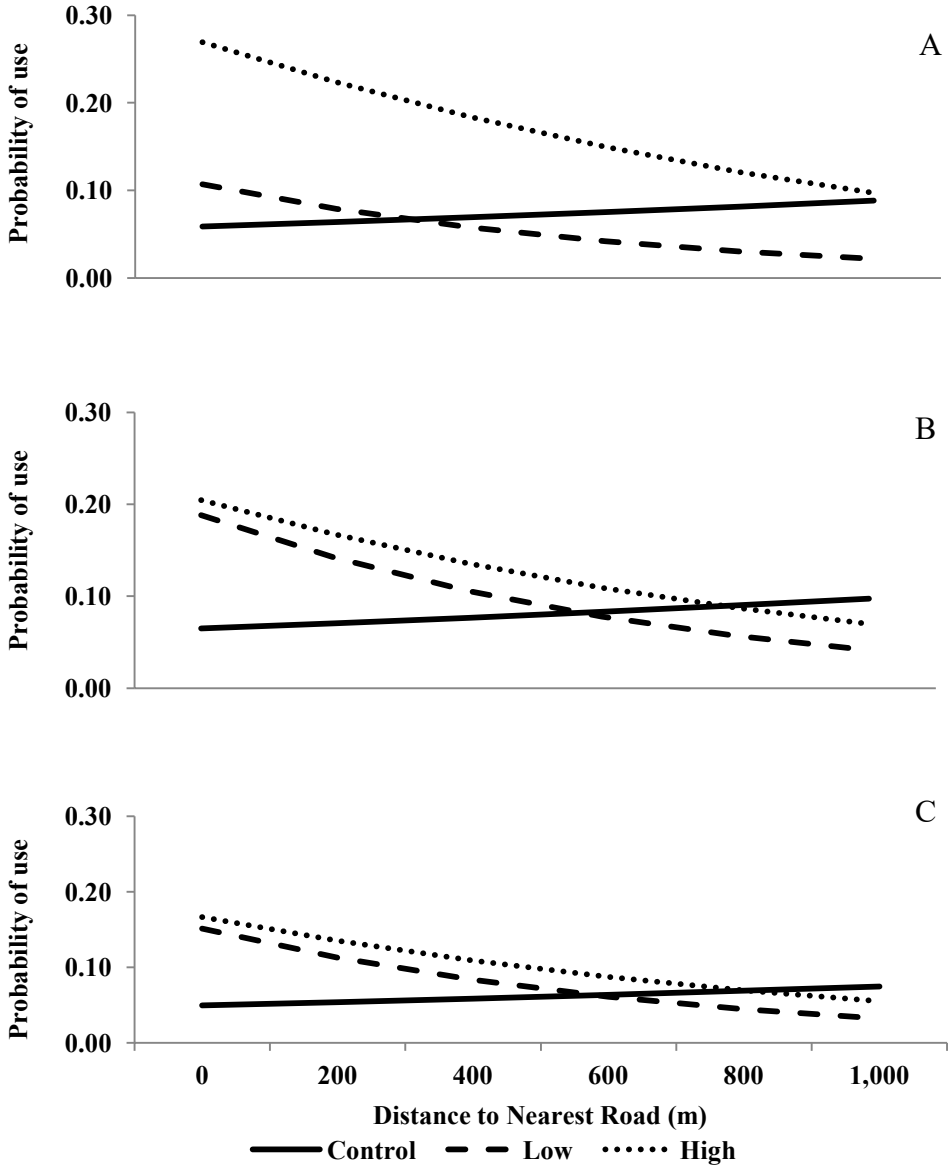

Figure 3.10. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1hunter/30 ha) and initial exposure (22-24 November 2008, 21-23 November 2009) on probability of use of areas closer to roads during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

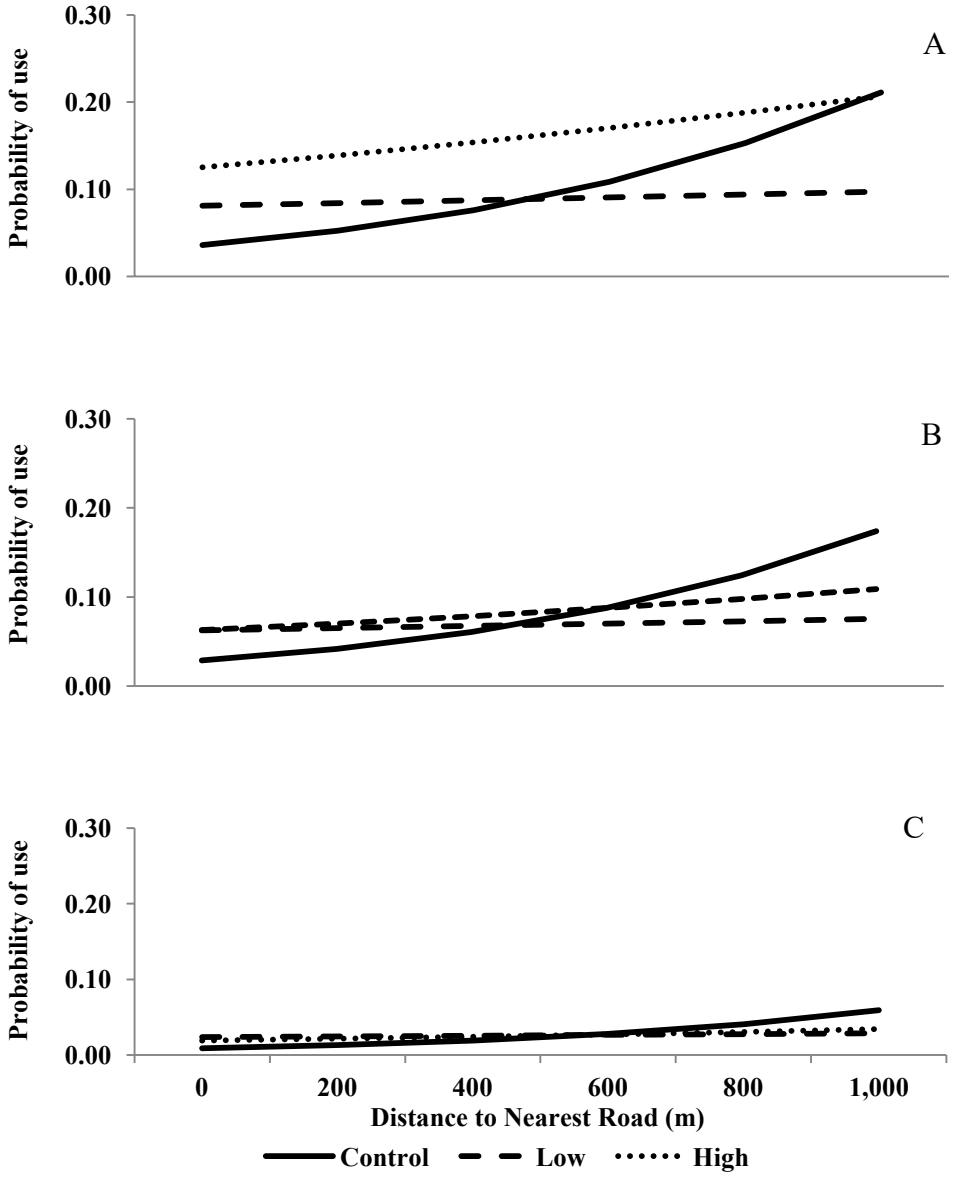

Figure 3.11. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of areas farther from roads during diurnal hours (0600-1800) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

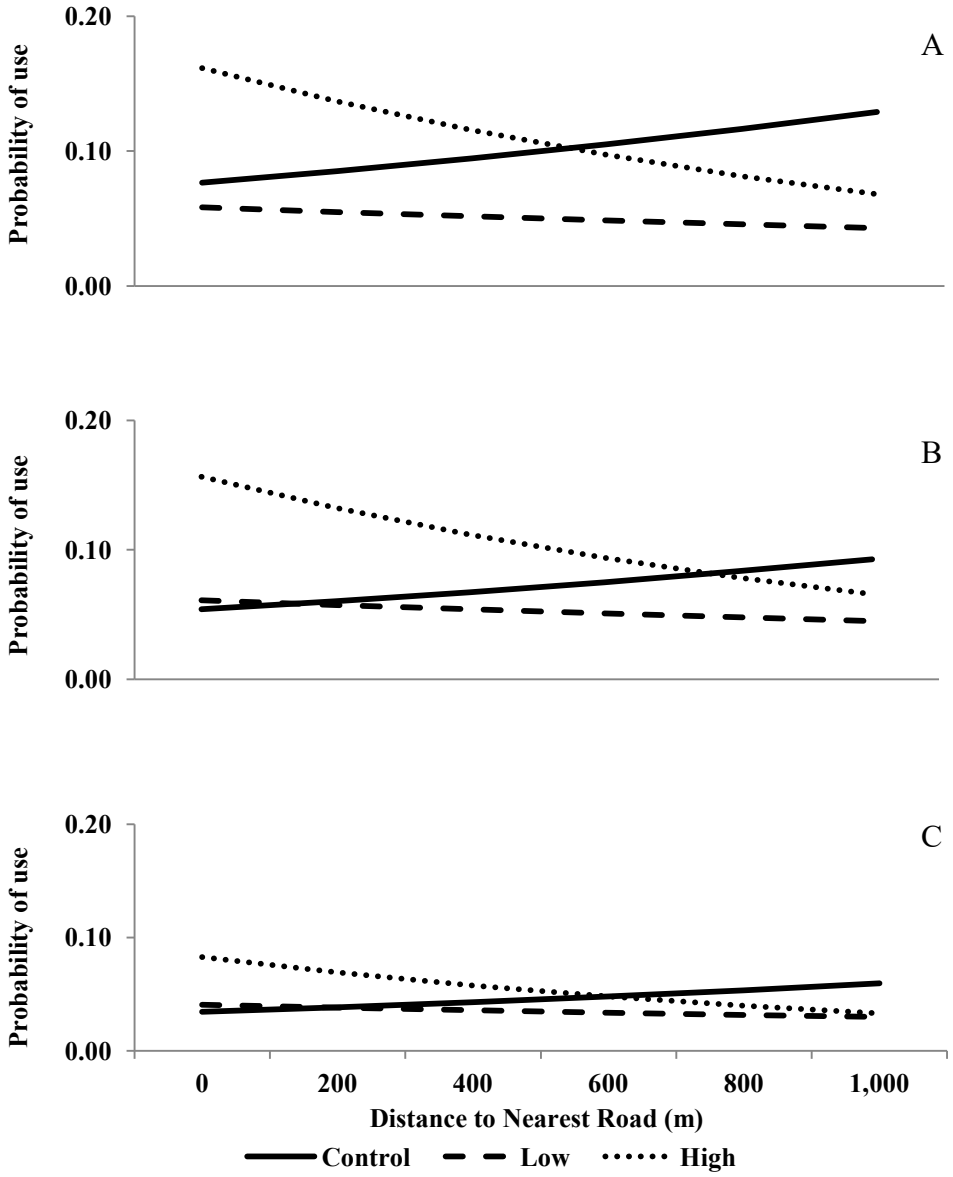

Figure 3.12. Effects of risk levels (control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and prolonged exposure (22-24 November 2008, 21-23 November 2009) on probability of use of areas closer to roads during nocturnal hours (1800-0600) within forested (A), mixed (B), and grassland (C) areas by adult, male white-tailed deer (≥ 2.5 years old) in south-central Oklahoma. For each landscape variable of interest, all other variables were held constant at their mean value while modeling the variable of interest across the observed values (x-axis scaled to observed values).

CHAPTER IV

HUMAN PREDATION RISK DECREASES OBSERVABILITY OF WHITE-TAILED DEER DURING HUNTING SEASON

ABSTRACT

With decline in large carnivores across much of North America, recreational hunters have become the primary management tool for ungulate populations. Although ungulates develop antipredator strategies to avoid encounters with natural predators, no one has addressed how exposure to the new top predator influences observation rates (i.e., index to harvest susceptibility) of white-tailed deer (*Odocoileus virginianus*) within the context of the risk-allocation hypothesis. I evaluated observation rates, movement distance, and resource selection of 37 adult (≥ 2.5 years) male deer at 2 risk levels (i.e., low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) and 2 exposure periods (initial = first weekend; prolonged = second and third weekends) on a 1,861-ha study area in Oklahoma during the 2008 and 2009 rifle deer seasons. Observed deer per hunter hour was greatest during initial exposure in low ($\bar{x}$ = 0.053, SE = 0.025) and high-risk levels ($\bar{x}$ = 0.053, SE = 0.013). However, observations declined during prolonged exposure in low ($\bar{x}$ = 0.015, SE = 0.009) and high-risk ($\bar{x}$ = 0.012, SE = 0.004). Despite increased hunter effort in the high-risk level, hunters observed a similar number of deer per hunter hour as the low-risk level. Movement distances of observed collared deer

were 1.6 and 1.8 times greater than unobserved deer leading up to and directly after the recorded hunter observation times, respectively ($F_{1,298} = 9.58$, $P = 0.002$). Use of higher elevations influenced observations of collared deer ($F_{1,298} = 3.71$, $P = 0.055$) but to a lesser extent than movement distance. Location of deer relative to other landscape features (i.e., vegetation type, slope, and distance from roads) did not affect probability of observation. I conclude that prey behaviorally adapt to human predation risk in a similar manner to natural predation by increasing antipredator behaviors to avoid encounters with humans.

INTRODUCTION

Predation risk assessment is central to prey species and shapes behaviors, morphology, and life history traits (Barbosa and Castellanos 2005, Brown and Chivers 2005). Risk assessment causes animals to learn to weigh risk of predation against various benefits when deciding which behavioral option to pursue (Lima and Bednekoff 1999). One area of behavioral ecology increasing in importance is effect of human predation risk on wildlife. Frid and Dill (2002) suggested that prey approached by humans likely respond similarly to those encountered by natural predators. However, little information exists on whether human predation risk within the context of recreational hunting can influence antipredator decision-making of white-tailed deer subsequently decreasing harvest susceptibility.

Previous research suggests that animals modify antipredator behaviors to account for risky situations by decreasing activity and foraging, and shifting habitat use to areas that reduce rates of detection or attacks by predators (Sih 1987, Lima and Dill 1990,

Lima 1998, Mirza et al. 2006). By increasing antipredator behaviors (e.g., decreased activity and foraging), prey can avoid immediate and possibly long term risk of predation, which leads to increased survivorship (Lima 1998). Increased survivorship evolves from an animal's ability to recognize the magnitude and temporal variation in risk in the environment (Lima and Bednekoff 1999).

Lima and Bednekoff (1999) recognized that theoretical models and empirical studies examining antipredator behaviors did not account for temporal variation in risk, which is an unavoidable aspect of most natural environments. This led them to develop the predation risk-allocation hypothesis, which accounts for magnitude and temporal variation in risk. Their hypothesis posits that prey living in safe environments with brief periods of risk should increase antipredatior behaviors (e.g., decreased activity and foraging) during risky situations, whereas, prey living in risky environments with brief periods of safety should decrease antipredator behaviors (e.g., increased activity and foraging) during safe times. However, if risk levels stay elevated for an extended period of time then prey are left with the choice of dying or increasing activity and foraging during risky times to meet energy requirements.

In today's ecosystems, in which humans have eliminated large carnivores, predation risk effects may occur because of recreational hunting (Ripple and Beschta 2004). Unfortunately, little is known about how white-tailed deer respond to human predation risk. Observation rates of deer by recreational hunters are used commonly to calculate survivability estimates, population size, and reproductive rates (Ericsson and Wallin 1999, Solberg and Saether 1999, Jacques et al. 2011). However, research is

needed to address if changes in number of observed deer have more to do with changes in population size, or, instead, with behavioral adaptations.

Understanding deer movement behaviors and use of landscape features may provide useful information regarding behavioral adaptations that allow some deer to go undetected during the hunting season. Predators may increase or decrease prey movement patterns (Abrams 2000, Sih and McCarthy 2002). Furthermore, landscape features (e.g., vegetative cover, elevation, slope, and roads) play an important role in predation risk (Kilgo et al. 1998, Ripple and Beschta 2004, Sawyer et al. 2006, Dzialak et al. 2011, Webb et al. 2011*a*). Documenting if deer behaviorally adapt to hunters will increase our knowledge of human predation risk assessment and aid in understanding behavioral ecology of white-tailed deer during the hunting season.

My research was designed to evaluate how deer perceive and respond to human predation risk during the hunting season by quantifying hunter observation rates and spatial ecology of deer within the context of the predation risk-allocation hypothesis. First, I evaluated changes in number of observed deer per hunter hour following initial exposure (i.e., first weekend) to human predation risk. I hypothesized that, following initial exposure, number of observations per hunter hour would decline across both treatments as deer increased their perception of human predation risk. Secondly, I examined number of deer observed per hunter hour in two risk levels (i.e., low- and high-risk) from initial to prolonged exposure. I hypothesized that the high-risk treatment would yield a greater number of observations per hunter hour than the low-risk treatment. Thirdly, I compared movement distances of observed and unobserved deer around the time of an observation. I hypothesized that probability of observing deer would increase

with increasing movement distance, which will likely cause deer to be more easily detected. Lastly, I evaluated influence of resource selection on observations of deer. I hypothesized that probability of observing deer would increase in open areas, higher elevations, gentle slopes, and areas closer to roads where visibility for hunters would be greatest.

STUDY AREA

I conducted this study on the Samuel Roberts Noble Foundation Oswalt Ranch (NFOR) in Love County located in south-central Oklahoma (Figure 2.1). The NFOR consists of 1,861 ha in the Cross Timbers and Prairies ecoregion, and contains oaks (*Quercus* spp.), elms (*Ulmus* spp.), hickories (*Carya* spp), ashes (*Fraxinus* spp.), hackberries (*Celtis* spp.), osage orange (*Maclura pomifera),* bluestems (*Andropogon spp.*), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans)*, and numerous forbs (Gee et al. 1994). The NFOR is rurally located, with minimal road density (1.4 km/km^2) bounding and within the study area. Elevation ranges from 233 m to 300 m and slope ranges from 0 degrees to 41 degrees (U.S. Department of Agriculture-National Cartography and Geospatial Center). During 2008 and 2009 study periods, rainfall ranged from 0 to 0.41 cm and mean temperature was 6.9° C (Burneyville, OK; Oklahoma Mesonet). During the study, NFOR was a non-operational ranch with no cattle grazing or prescribed fire management. Lease hunting ($\bar{x}$ = 5 hunters) ended after the 2006 hunting season to minimize effects of previous hunting exposure on study animals. Coyotes (*Canis latrans*) occurred on the study area.

The NFOR was broken into no risk (control = 679 ha), low-risk (1 hunter/101 ha; 585 ha), and high-risk (1 hunter/30 ha; 583ha) treatments based on existing landscape features, property boundaries, and fencing, with the goal of producing 3 areas of similar size and vegetative composition (Figure 2.1). Vegetative composition (i.e., forest, mixed forest/grassland, and grassland) was similar across all three treatments. I divided the low- and high-risk treatments into smaller hunter compartments comparable to the desired risk levels, which distributed hunter effort uniformly within each treatment. I randomly relocated treatments during the second year, which shifted the treatments clockwise to create temporal replication (Morrison et al. 2010). Surrounding properties had a variety of hunting effort applied each year, ranging from none to high-risk.

METHODS

Capture and Handling

I captured 52 adult male white-tailed deer (≥ 1.5 years of age) during winters of 2008 (n = 25) and 2009 (n = 27) using drop nets (Gee et al. 1999). I aged deer according to tooth replacement and wear (Severinghaus 1949), but due to variations in wear patterns (Gee et al. 2002), I classified them as ≥ 1.5 years at capture, and all deer were ≥ 2.5 years of age by the study period. I sedated deer with an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Kreeger 1996). I weighed, ear-tagged, and affixed each deer with a GPS collar (ATS G2000 Remote-Release GPS, Advanced Telemetry Systems, Isanti, MN). I chose to use cattle-grade ear tags (4 inches x 3 inches) for ease in identification in the following colors: black with white lettering, yellow with black lettering, and green with black lettering. The Institutional Animal Care and Use

Committee at Mississippi State University approved all capture, handling, and marking techniques (Protocol 07-034).

I programmed GPS collars to collect location estimates every 8 minutes from 7 November through the end of the study (6 December 2008 and 7 December 2009). Each location included Universal Transverse Mercator coordinates, date, time, fix status, position dilution of precision, and horizontal dilution of position. A mortality sensor indicated inactivity after 8 hours. I monitored deer once monthly from 1 February to 31 October (2008-2009) and once weekly from 1 November through end of firearms season (6 December 2008 and 7 December 2009) to determine general location of deer and mortalities. I removed 3-dimensional fixes with position dilution of precision values > 10 and 2-dimensional fixes with position dilution of precision values > 5 (Moen et al. 1997, Dussault et al. 2001, D'Eon and Delaparte 2005).

Prey Exposure and Hunter Effort

An assumption of the predation risk-allocation hypothesis is prey can adequately discriminate between changes in magnitude and temporal variation in risk; however, prey likely require a period of exposure to predation risk to fully recognize the amount and time of risk. (Lima and Steury 2005). To allow adult male deer to discriminate between the magnitude and temporal variation in risk, I considered the first hunted weekend as initial exposure to human predation risk (i.e., 22-23 November 2008, 21-22 November 2009) followed by prolonged exposure (i.e., second and third weekends; 28-30 November 2008, 6-7 December 2008; 27-29 November 2009, 5-6 December 2009) (Ferrari et al.

2009). I focused this study on weekends during the 16 day hunting season because I was able to maintain differences between low- and high-risk levels.

Hunter effort provided a metric of general hunting pressure across low- and high-risk levels during initial and prolonged exposure. I required hunters to spend at least 4 hours each day on the weekend in their hunting compartment. I calculated hunter effort (i.e., hours/day) by totaling number of hours hunted in each treatment during initial and prolonged exposure.

Hunter Observations as Index to Harvest Susceptibility

To evaluate effects of hunting pressure and exposure on number of deer observed per hunter hour, I required hunters to keep detailed records of collared deer sightings, recording ear tag color, number, and time seen. Additionally, all hunters were supplied with a Garmin Etrex Venture GPS unit (Garmin, Olathe, KS) to track their locations (i.e., fix acquired every 1-minute). To ensure correct identification of collared deer, I included only hunter observations that occurred during legal shooting hours (i.e., 1/2 hour before sunrise and 1/2 hour after sunset). Furthermore, I validated hunter observations of deer using GPS locations of deer and hunters within ArcGIS 9.3 (ESRI, Inc., Redlands, CA).

Spatial Ecology of Observed and Unobserved Deer

Deer movement behavior and resource selection were affected by risk levels, temporal variation in risk, and exposure to human predation risk (see Chapters 2 and 3). Variation in movement distance and resource selection may lead to some deer being observed and some deer going undetected. To determine if movement distance and resource selection influenced observation of collared deer, I used ArcGIS 9.3 and hunter

observation data to determine the closest observed and unobserved GPS locations leading up to (i.e., 5 to 8 minutes) and directly following (i.e., 0 to 7 minutes) the recorded observation time. If there was a missed GPS location around the exact time of observation, I used the next closest location in time. However, I required all locations to fall within 1/2 hour on either side of the hunter's recorded observation time to encompass the majority of human recording error. For example, if deer 34 was observed at 7:05 a.m., I classified the location prior to the observation (e.g., 6:58 a.m.) and the location directly following the observation (e.g., 7:06 a.m.). Moreover, I classified all unobserved locations prior to and directly following the recorded observation time that fell within 1/2 hour of 7:05 a.m. (e.g., 6:35 to 7:35).

Due to the complexity of the data, I had several cases that required special classification. First, in cases where multiple deer were observed within minutes of each other by different hunters, I did not permit these observed deer to be classified as unobserved within the same hour. This approach therefore reduced any confounding effects of associating behavior or resource selection of an observed deer to the category of unobserved deer. Second, I allowed unobserved deer to be classified more than once per hour in cases where multiple deer were observed within an hour but at different 8-minute intervals. Unobserved deer were chosen by locating the location nearest to the recorded observation. In essence, this analysis was attempting to capture why certain deer were observed whereas other deer were not based on behavior (i.e., movement distance) and resource selection. Third, there were several instances where a hunter recorded multiple observations of the same deer within minutes of each other; therefore, I chose the first observed time for the analysis to avoid pseudoreplication. For instance, a

deer may have been observed feeding and remained relatively stationary for a period of time; therefore, I omitted observations by the same hunter when the deer was present (without leaving and returning). Last, in cases where a location occurred 4 minutes on either side of the recorded time, I selected the location that was 13-16 minutes prior to the observation because 4 minutes on either side of the observed time would not fully capture a deer's activity leading up to the recorded observation time.

To characterize movement behavior of observed and unobserved deer that may influence observation susceptibility, I calculated 8-minute movement distances of all observed and unobserved deer leading up to the recorded observation time using the Animal Movement extension within Hawth's Tools in ArcGIS 9.3 (Beyer 2004). This tool calculates step length (i.e., distance between successive points). Greater movement distance of observed deer leading up to the recorded observation time may increase the probability of detection. Furthermore, I calculated movement distances directly following the recorded observation time. Using these distances, I compared movement behavior prior and directly following the recorded observation time to assess if hunters influenced movements after observation, which may result in greater antipredator behavior (i.e., flight distance as calculated by movement distance).

Landscape Classification

To evaluate influence of variable resource selection at time of observation, I used the closest location to recorded observation time of observed and unobserved deer. For example, some deer may be observed more often under certain conditions such as when using grasslands or areas closer to roads. I addressed the question of resource selection of

observed and unobserved deer by developing a vegetation type map. Using 2009 growing-season National Agriculture Imagery Program aerial imagery, I re-sampled a 1-meter resolution grid into a 17-m resolution grid using ERDAS Imagine 9.3 (ERDAS, Inc, Atlanta, GA) software. I reclassified to 17-m resolution based on fractal analyses (Webb et al. 2009) because that was the smallest patch size perceived by deer and because most location errors were ≤ 3.7 m.

Based on spatial scale and vegetative structure of the study area, I classified 3 vegetative cover types: forest, mixed forest/grassland (hereafter mixed), and grassland. I classified forested areas as having greater than 70% closed canopy cover, grasslands as having greater than 70% open areas, and mixed forest/grassland areas as having less than 70% of closed canopy (i.e., forest) and open areas (i.e., grassland). I measured visual obstruction at 90 stratified randomly placed vegetation plots (i.e., 30 in each cover type) using a 1.8-m Nudds density board (Nudds 1977) separated into 6 equal 0.3-m sections. The board was viewed from a distance of 10-m in each cardinal direction by a standing observer from a standardized height of 1.5-m and obstruction of each section was estimated in 20% increments.

I conducted a supervised classification based on spectral signatures of known forest, mixed, and grassland areas. I calculated a zonal majority and majority fraction based on the 1-m imagery to classify each 17-m pixel into either forest, mixed, or grassland vegetative types (Lillesand et al. 2004). These functions compute the most commonly occurring value in each zone (17-m cell) and the fraction of the total zone that is occupied by the majority class. I masked roads, non-vegetation areas, and water before performing the supervised classification on the vegetation areas to prevent misclassifying

these areas as a vegetation type. To evaluate accuracy of the supervised classification, I compared the re-classified image to 90 stratified randomly placed vegetation plots (i.e., 30 in each cover type).

I obtained a 10 m resolution DEM from the U.S. Department of Agriculture-National Cartography and Geospatial Center (2009) and calculated elevation and degree of slope using Spatial Analyst in ArcGIS 9.3. I extracted values for each observed and unobserved deer location with the vegetation type (i.e., mixed = 1, forest = 2, and grassland = 3), elevation, and slope map layers using Intersect to Point within Hawth's Tools. Moreover, I delineated roads (i.e., dirt, stone, and paved) bounding and within the study area that hunters used to travel to their hunting compartments. These roadways received greatest traffic during early morning and evening hours when hunters were entering and leaving the field. Using ArcGIS 9.3, I spatially joined all deer locations to the nearest roadway.

Statistical Analysis

Descriptive statistics

I evaluated changes in number of deer observed per hunter hour by dividing total number of deer (i.e., including repeated observations of the same deer) observed each day by hunter effort in low- and high-risk levels during 2008 and 2009. I calculated mean number of deer observed per hunter hour during each exposure period (i.e., initial = first weekend; prolonged = second and third weekends). Furthermore, I report number of observed and unobserved collared deer available to be seen by exposure period. I assume observation rate can be used as an index to harvest susceptibility.

Visual obstruction

Classification of vegetation types corresponded to visual obstruction, which provided a range of percentage of obstruction for each vegetation type. I analyzed estimates using the mid-point of each range at the estimated coverage, yielding maximum obstruction of 90%. I used a general linear model to test for differences in percentage visual obstruction. I compared means among forest, mixed, and grassland habitat types in PROC GLM (SAS Institute Inc. 2003).

Logistic regression

I used generalized linear mixed models (GLMM; PROC GLIMMIX) and a logistic regression framework to determine what factors influenced the probability of observing collared deer. I evaluated movement distances leading up to the recorded observation time, which will likely influence the probability of observation. Whereas, evaluating resource selection closest to recorded observation (i.e., directly after) time will yield types of resources that influence the probability of observation. Data was analyzed as a binomial response variable (1 = observed; 0 = unobserved), which yields values proportional to the probability of use of a resource unit (Boyce et al. 2002). I included year and deer identification as random effects to account for unmeasured environmental variation, similarity of data within years, and correlation within individual animals. For the GLMM, I used a binary distribution, logit-link function and a variance components covariance structure for random effects. Logistic regression is a simplistic approach to analyzing probability of resource selection and is used widely for other statistical

analyses in biology (Manly et al. 2002). Because of the lack of research on this topic, I used $\alpha = 0.10$ for all statistical tests reduce the chance of Type II error (Tacha et al. 1982).

RESULTS

I deployed 52 collars (25 in 2008, 27 in 2009) on adult male deer during the study. However, I analyzed data on 19 collars in 2008 and 18 collars in 2009, with 7 deer analyzed in both years. Fifteen deer were not included due to illegal harvest (n = 8), legal harvest (n = 1), mechanical failures of the collar (n = 3), natural mortality (n = 1), deer-vehicle collision (n = 1), and dispersal from the study area (n = 1). One of the 8 illegally harvested deer required development of an underwater antenna to retrieve the collar from a pond (Webb et al. 2011*b*). I used 682 8-minute locations leading up to (observed = 47; unobserved = 291) and directly following (observed = 48; unobserved = 296) the recorded hunter observation times to examine the spatial ecology of observed and unobserved deer. GPS collars averaged 96.8% (SD = 9.8) fix success and a 3.7-meter (SD = 7.6) error.

Hunter Effort

Hunter effort averaged 30 hrs/day in the low-risk treatment and 109 hrs/day in the high-risk treatment during the study period. Hunter effort declined between initial exposure (i.e., first weekend of hunting) and prolonged exposure (i.e., last 2 weekends of hunting) in both treatments: low-risk declined by 9.4% from 32 to 29 hrs/day and high-risk declined by 19.8% from 127 to 102 hrs/day However, hunters continued to provide a significant hunting threat during the prolonged exposure with 291 and 1,024 hunter hours spent afield in the low- and high-risk areas, respectively.

Hunter Observations as Index to Harvest Susceptibility

Hunters in the low-risk treatment observed 4 out of 14 (28.6%) individual collared deer available to be seen during initial exposure (i.e., first weekend). Of the 4 collared deer observed, 3 were seen once and 1 was seen twice. Ten out of 14 (71.4%) collared deer were not seen during initial exposure. In contrast, hunters in the high-risk observed 9 out of 17 (53.0%) individual collared deer during initial exposure of which 2 were seen once, 3 twice, 1 3 times, 2 4 times, and one 5 times. Eight out of 17 (47.0%) collared deer were not seen during initial exposure. During the prolonged exposure (i.e., last 2 weekends), low-risk hunters observed 4 out of 13 (30.8%) individual collared deer. Of the 4 collared deer observed, 3 were seen once and one was seen twice. Nine out of 13 (69.2%) collared deer were not seen during prolonged exposure. High-risk hunters observed 8 out of 15 (53.3%) collared deer during prolonged exposure; however, 7 out of 15 (46.7%) deer were never seen by hunters despite being available for observation. Of the 8 collared deer observed, 6 were seen once and 2 were seen 3 times.

Number of observations of collared deer per hunter hour (i.e., including repeated observations of the same deer) in the low-risk level declined from initial ($\bar{x}$ = 0.053, SE = 0.025) to prolonged exposure ($\bar{x}$ = 0.015, SE = 0.009). A similar decline was seen in the high-risk level from initial ($\bar{x}$ = 0.053, SE = 0.013) to prolonged exposure ($\bar{x}$ = 0.012, SE = 0.004). Despite increased hunter effort in the high-risk level, hunters observed similar number of deer per hunter hour as the low-risk level.

Spatial Ecology of Observed and Unobserved Deer

Visual obstruction differed among the 3 vegetation types ($F_{2,87} = 150.35$, $P < 0.001$). Visual obstruction increased from grasslands ($\bar{x}$ =18.5, SE =1.3) to mixed ($\bar{x}$ =59.5, SE = 2.3) to forested ($\bar{x}$ = 68.0, SE = 2.7) areas, supporting the separation of forest, mixed, and grassland areas. Furthermore, using these vegetation plots (i.e., 30 in each cover type), I correctly classified forested (83.3%), mixed (82.8%), and grassland (81.5%) areas. Overall classification accuracy and kappa statistics were 86.1% and 0.83, respectively.

Movement distance ($F_{1,298} = 9.58$, $P = 0.002$) and elevation ($F_{1,298} = 3.71$, $P = 0.055$) influenced the probability that a collared deer was observed. Both movement distance ($\beta = 0.005$, SE = 0.002) and elevation ($\beta = 0.029$, SE = 0.015) had a positive relationship with probability of being observed. However, vegetation type ($F_{2,298} = 2.23$, $P \geq 0.109$), distance to nearest road ($F_{1,298} = 0.94$, $P \geq 0.333$), slope ($F_{1,298} = 0.09$, $P \geq 0.759$) did not influence probability of deer being observed. Based on standardized coefficient estimates, movement distance and elevation were the most important characteristics that influenced observations of collared deer.

Average 8-minute movement distance leading up to the observation of collared deer was 123.1 m (95% CI: 93.4 - 152.8), which was similar to movement distance directly following the observation ($\bar{x}$ = 124.7 m; 95% CI = 95.0 - 154.4). However, when comparing movement distance of observed deer to unobserved deer prior to an observation, deer that were not observed moved 38.3% less during 8-minutes ($\bar{x}$ = 75.9 m, 95% CI = 62.5-89.3). The same pattern held for unobserved deer when considering

movement following an observation event; unobserved deer continued to move less than deer that were observed ($\bar{x}$ = 69.1 m, 95% CI = 55.7-82.4).

Elevation was the second most important landscape feature to influence observation of collared deer. Average elevation used by collared deer closest (i.e.., directly following) to the hunter observation was 267.8 m (95% CI = 263.5-272.2), whereas unobserved deer used an average elevation of 264.7 m (95% = 263.1-266.2). However, this change was of lesser importance than movement distance.

DISCUSSION

As predicted, increased predator density resulted in a greater initial detectability, although observations in both treatments declined during prolonged exposure to hunters. Previous research has shown that increasing hunter pressure will cause deer to move more (Heberlein and Kuentzel 2002) and increase harvest susceptibility (McCullough et al. 1990, Fryxell et al. 1991, Roseberry and Woolf 1991, Broseth and Pedersen 2000); however, these studies did not address prolonged exposure to greater hunter densities which can cause fewer encounters with humans similar to my findings. Furthermore, lesser hunter densities may not induce sufficient deer movement to maximize vulnerability (Foster et al. 1997, Heberlein and Kuentzel 2002). Although, depending on management goals, low-risk levels may be preferred to avoid significantly affecting deer behaviors. Furthermore, my data suggests that deer learn to recognize and adapt to predation risk following initial exposure, which led to a decline in observations, as supported by the predation risk-allocation hypothesis.

Observation rates (i.e., index to harvest susceptibility) decreased following initial exposure as deer learned that recreational hunters posed a predation risk threat. Previous research has used hunter observations to understand survival, population size, and reproductive rates of ungulates (Ericsson and Wallin 1999, Solberg and Saether 1999, Jacques et al. 2011). Potential for human bias in observations throughout the season, however, may lead to erroneous conclusions about survival, population size, and reproductive rates. Furthermore, the decline in observations during prolonged exposure is likely due to decreased movements, which likely reduce potential encounters with hunters. Previous research has shown that deer decrease movement rates following 3 days of exposure to human predation risk (see Chapter 2). Moreover, my results are consistent with previous studies that found a decline in observations after a short temporal period; Van Etten et al. (1965), Murphy (1965), and Grau and Grau (1980) found similar declines in hunter observations of deer. Reduction in observations later in the season are likely influenced by an increased wariness of hunters (Sage et al. 1983) and needs to be considered when using hunter observations to assess herd dynamics.

High-risk hunters observed a greater number of deer compared to the low-risk; however, number of observed deer per hunter hour indicates that high-risk levels may not lead to increased observations over time. Grau and Grau (1980) found hunter effort increased later in the season but resulted in fewer observations as deer avoided encounters with humans. Despite greater effort in the high-risk level, my results indicate that lower levels of hunting pressure may provide a greater observation rate over time compared to high-risk levels. Lower risk levels may not induce sufficient alterations in movement behaviors, which may influence observability (Heberlein and Kuentzel 2002).

Furthermore, deer movement behaviors in the low-risk level were similar to the control treatment (i.e., no risk; Chapter 2), which indicates low levels of hunting pressure can still lead to observations of collared deer.

Despite these changes in antipredator behavior, observed deer had greater movement distances than unobserved deer, indicating that greater movement contributed to observability. Previous research has shown that moving prey (i.e., observed deer) are more easily detected by predators, which also explains the smaller movement rates for unobserved deer (Lima and Dill 1990). Furthermore, this decline in harvest susceptibility does not imply that a deer herd is overharvested but rather deer are responding to human predation risk by avoiding contact with hunters (Van Etten et al. 1965). Similarly, animals modify behavior to account for predation risk by increasing vigilance, reducing activity, decreasing foraging, and shifting use to habitats that reduce rates of detection or attacks by predators (Ydenberg and Dill 1986, Lima and Dill 1990, Sih and McCarthy 2002). However, my results indicate that resource selection played a lesser role in observability of collared deer.

Use of higher elevations influenced observability of collared deer during the study period. My results indicate only a 3 meter difference in use of higher elevations by observed collared deer compared to unobserved deer. However, elevational change across the study area was minimal; thus, a 3 meter change is likely a significant biological effect. Furthermore, deer may have been attempting to use these higher elevations to avoid risk of predation (Bergerud and Page 1987, Lingle 2002, Kittle et al. 2008) and inadvertently were observed by hunters that were located in higher elevations. Despite

these findings, elevation played a lesser role in observability compared to movement distance.

This study demonstrated that deer increased antipredator behaviors to avoid immediate predation risk; however, prior experience with hunting pressure may have modified their behaviors. Prey animals continually modify their responses to predation risk, and much of this change can be attributed to their ability to learn (Brown and Chivers 2005). Although there was no hunting on the study area one year prior, deer studied in this project had at least one year of possible hunter pressure experience as fawns and potentially at other ages on adjacent properties and during the first year of data collection. Thus, my study animals likely were not totally naïve to recreational hunting risk. Illegal harvest of 8 animals prior to the legal firearms season indicates there was also risk outside of the legal firearms season. These learned experiences may also have attributed to the lack of predator density effect on movement rates. Predation risk is extremely variable throughout time with risk changes occurring year to year, season to season, day to day, and even moment to moment, which causes prey to fine tune predator avoidance strategies to recent experiences (Brown and Chivers 2005).

Overall, this study provides evidence that human predation risk can lead to a decrease in observability of adult, male white-tailed deer during the hunting season. Additional research is needed to address different lengths of initial hunter exposure on observation rates, which will help researchers, biologists, and land managers develop an appropriate time table as to when they can evaluate herd dynamics (e.g., population size, buck to doe ratio, etc.) during the hunting season without jeopardizing integrity of collected data. Furthermore, research is needed to evaluate whether maintaining low-risk

levels during longer hunting seasons increase harvest susceptibility because deer faced with low predation risk were less likely to exhibit heightened antipredator behaviors in my study.

ACKNOWLEDGEMENTS

This study was funded by the Samuel Roberts Noble Foundation and Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture. Samuel Roberts Noble Foundation provided the study site and recruited employees, family, and friends to participate in hunting the property. R. Stevens, D. Payne, and F. Motal provided technical and field assistance. This is Mississippi State University Forest and Wildlife Research Center publication number WF-XXX.

LITERATURE CITED

Abrams, P. A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. Ecology 81:2902-2913.

Barbosa, P., and I. Castellanos, editors. 2005. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Bergerud, A.T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology 65:1597-1606.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed May 1, 2009.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.

Broseth, H., and H. C. Pedersen. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS, and GIS. Journal of Applied Ecology 37:182-190.

Brown, G. E., and D. P. Chivers. 2005. Learning as an adaptive response to predation. Pages 34-54 *in* P. Berbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, Inc., New York, New York, USA.

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

Dussault, C., R. Courtois, J.P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. Wildlife Society Bulletin 29:171-179.

Dzialak M.R., S.M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE 6: e14597.

Ericsson, G., and K. Wallin. 1999. Hunter observations as an index of moose *Alces alces* population parameters. Wildlife Biology 5:177-185.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Foster, J. R., J. L. Roseberry, and A. Woolf. 1997. Factors influencing efficiency of white-tailed deer harvest in Illinois. Journal of Wildlife Management 61:1091-1097.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1-16.

Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management 55: 377-385.

Gee, K. L., M. D. Porter, S. Demarais, F. C. Bryant, and G. Van Vreede. 1994. White-tailed deer: their foods and management in the Cross Timbers. Second edition. Samuel Roberts Noble Foundation Publication, Ardmore, Oklahoma, USA.

Gee, K. L., J. H. Holman, and S. Demarais. 1999. A man-power efficient drop-net system for capturing white-tailed deer. 22nd Annual Southeast Deer Study Group Meeting 22:31.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387-393.

Grau, G. A., and B. L. Grau. 1980. Effects of hunting on hunter effort and white-tailed deer behavior. Ohio Journal of Science 80:150-156.

Heberlein, T. A., and W. F. Kuentzel. 2002. Too many hunters or not enough deer? Human and biological determinants of hunter satisfaction and quality. Human Dimensions of Wildlife 7:229-250.

Jacques, C. N., T. R. Van Deelen, W. H. Hall, Jr., K. J. Martin, and K. C. Vercauteren. 2011. Evaluation how hunters see and react to telemetry collars on white-tailed deer. Journal of Wildlife Management 75:221-231.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359-1364.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157:163-175.

Kreeger, T. J. 1996. Handbook of Wildlife Chemical Immobilization. Veterinary Services. Wildlife Pharmaceuticals, Fort Collins, Colorado, USA.

Lillesand, T., R. Kiefer, and J. Chipman. 2004. Remote sensing and image interpretation. Fifth Edition. John Wiley and Sons, Inc., New York, New York, USA.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215-290.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and T. D. Steury. 2005. Perception of predation risk: the foundation of nonlethal predator-prey interactions. Pages 166-188 *in* P. Barbosa and I. Castellanos, editors. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83:2037-2048.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Press, New York, New York, USA.

McCullough, D. R., D. S. Pine, D. L. Whitmore, T. M. Mansfield, and R. H. Decker. 1990. Linked sex harvest strategy for big game management with a test case on black-tailed deer. Wildlife Monographs 112:3-41.

Mirza, R. S., A. Mathis, and D. P. Chivers. 2006. Does temporal variation in predation risk influence the intensity of antipredator responses? A test of the risk allocation hypothesis. Ethology 112:44-51.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.

Morrison, M. L., W. M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2010. Wildlife study design. Springer Science and Business Media, New York, New York, USA.

Murphy, D. A. 1965. Effects of various opening days on deer harvest and hunting pressure. Proceedings of the Annual Conference of the Southeastern Association of Game and FishCommissioners 19:141-146.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113-117.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Roseberry, J. L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117:3-59.

Sage, R. W., Jr., W. C. Tierson, G. F. Mattfeld, and D. F. Behrend. 1983. White-tailed deer visibility and behavior along forest roads. Journal of Wildlife Management 47:940-953.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195-216.

Sih, A. 1987. Direct and indirect impacts on aquatic communities. University Press of New England, New Hampshire, USA.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437-443.

Solberg, E. J., and B. E. Saether. 1999. Hunter observations of moose *Alces alces* as a management tool. Wildlife Biology 5:107-117.

Tacha, T C., W. D. Wade, and K. P. Burnham. 1982. Use and interpretation of statistics in wildlife journals. Wildlife Society Bulletin 10:355-362.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59-73.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210-1217.

Webb, S. L., M. R. Dzialak, R. G. Osborn, S. M. Harju, J. J. Wondzell, L. D. Hayden-Wing, and J. B. Winstead. 2011*a*. Using pellet groups to assess response of elk and deer to roads and energy development. Wildlife Biology in Practice 1:32-40.

Webb, S. L. J. A. Gaskamp, K. L. Gee, S. Demarais, and A. R. Little. 2011*b*. Design of an underwater telemetry antenna for locating and retrieving submerged radiocollars. Wildlife Society Bulletin 35:101-104.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advanced Study Behaviour 16:229–249.

CHAPTER V

SYNTHESIS AND RECOMMENDATIONS

Predation risk assessment is central to the lives of most species and acts as a strong selective pressure on prey behavior (Barbosa and Castellanos 2005, Ferrari et al. 2009). This selective pressure has changed over time for ungulates with elimination of large carnivores and replacement by human hunters (Ripple and Beschta 2004). Previous research has suggested that animals approached by humans will likely respond similarly to those encountered by natural predators (Frid and Dill 2002). However, little empirical information exists on how humans affect antipredator decision-making of white-tailed deer (*Odocoileus virginianus*). Moreover, understanding how humans fill this role as top predator is necessary for advancing our knowledge of behavioral ecology and development of proper wildlife management programs.

Adult, male white-tailed deer recognized human predation risk by altering movement behaviors and resource selection with greater predator density during prolonged exposure. My results reveal that 1 hunter per 30 hectares (i.e., high-risk) provided enough human disturbance to cause deer to alter their antipredator behaviors, whereas, 1 hunter per 101 hectares (i.e., low-risk) appears to be below the threshold needed to significantly alter antipredator behaviors. Furthermore, I suggest that future

research examine where the magnitude of risk threshold exists between low- and high-risk levels. Overall, these results support the predation risk-allocation hypothesis.

If the goal of management is to observe more adult male deer, the assumption that increasing hunter density will lead to a greater number of deer observations may not be fully accurate. My results suggest deer learn to adapt to human predation risk by altering movement behaviors and resource selection, which likely influenced the decline in collared deer observations (i.e., index to harvest susceptibility) in the high-risk treatment. Similarly, maintaining or increasing hunting pressure later in the season will likely lead to a decrease in success and increased wariness towards humans (Altmann 1958, Van Etten et al. 1965, Grau and Grau 1980). However, maintaining low levels of hunting pressure (e.g., 1 hunter/ 101 ha) may result in a greater number of observations over an extended period of time because of the lack of significant human disturbance.

Harvest susceptibility primarily depends on density and distribution of hunters (Harden et al. 2005); however, antipredator behaviors exhibited by deer also may influence susceptibility. In my study, deer increased antipredator behaviors by decreasing movement behaviors and space use while increasing their use of security cover, which likely influences harvest susceptibility. Observational data collected by recreational hunters are commonly used to calculate survivability estimates, population size, reproductive rates, and it's typically inexpensive (Ericsson and Wallin 1999, Solberg and Saether 1999, Winchcombe and Ostfeld 2001, Jacques et al. 2011). However, increased antipredator behaviors directly following 3 days of human predation risk led to a decline in observations of collared deer. This decline indicates that observational data used to examine herd dynamics may not be completely reliable after 3 days of exposure to human

predation risk. If biologists and land managers want to address herd dynamics using observational data then increased hunter density over a short period of time may achieve this goal.

Temporal variation in risk influenced movement behaviors and resource selection during the study period; however, deer were unable to fully recognize when hunters were present or absent. Lima and Bednekoff (1999) predicted that prey should increase activities and foraging during periods of safety (i.e., nocturnal hours) within risky environments. Contrary to their hypothesis, deer decreased their movement behaviors and showed an increase in use of security cover during nocturnal hours. These results may indicate that deer were maintaining a heightened level of vigilance due to a potential lack of knowledge of whether hunters were still present or not. Furthermore, I suggest that that future human predation risk studies need to focus on different lengths of exposure to risk levels to provide prey with an adequate assessment of temporal variation in risk.

Predation risk caused by humans is an important ecological concept that needs to be addressed with additional research. With the loss of large carnivores and replacement by human hunters, the management of white-tailed deer strongly relies on human predation to keep herds within the carrying capacity of the land. Increasing urbanization, fragmentation of habitats, and loss of hunters in recent years requires that we achieve a better understanding of how game animals perceive humans. Future research examining the role of human predation risk and its effect on deer and other wildlife will increase our knowledge of antipredator decision-making in the presence of humans, which can lead to more informed management decisions.

LITERATURE CITED

Altmann, M. 1958. The flight distance in free-ranging big game. Journal of Wildlife Management 22:207-209.

Barbosa, P., and I. Castellanos, editors. 2005. Ecology of predator-prey interactions. Oxford University Press, New York, New York, USA.

Ericsson, G., and K. Wallin. 1999. Hunter observations as an index of moose *Alces alces* population parameters. Wildlife Biology 5:177-185.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:1-16.

Grau, G. A., and B. L. Grau. 1980. Effects of hunting on hunter effort and white-tailed deer behavior. Ohio Journal of Science 80:150-156.

Harden, C. D., A. Woolf, and J. Roseberry. 2005. Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. Wildlife Society Bulletin 33:233-242.

Jacques, C. N., T. R. Van Deelen, W. H. Hall, Jr., K. J. Martin, and K. C. Vercauteren. 2011. Evaluation how hunters see and react to telemetry collars on white-tailed deer. Journal of Wildlife Management 75:221-231.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649-659.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Root, B. G., E. K. Fritzell, and N. F. Giessman. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin. 16:145-151.

Solberg, E. J., and B. E. Saether. 1999. Hunter observations of moose *Alces alces* as a management tool. Wildlife Biology 5:107-117.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59-73.

Winchcombe, R. J., and R. S. Ostfeld. 2001. Bowhunter observation versus spotlighting as an index to deer abundance. Northeast Wildlife 56:39-48.