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Efficacy of Predator Exclusion Methods and Id of Nest Predators for Interior Least Terns and Piping Plovers at Off-Channel Nesting Sites along the Central Platte River, Nebraska, Usa

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EFFECTS OF HUNTER MOVEMENT AND HABITAT USE ON OBSERVATION RATE OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

A Thesis
Presented to the
Graduate Faculty of the Biology Department
and the
Faculty of the Graduate College
University of Nebraska

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
University of Nebraska – Kearney

By:
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July 2021

THESIS ACCEPTANCE

Acceptance for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree, Master of Science, University of Nebraska at Kearney.

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23 June 2021
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DEDICATION

This thesis is firstly dedicated to my entire family: my parents Keith and Virginia who always cultivated my passions and encouraged me, and my sister Jaime who taught me what true resilience looks like. Secondly, I would like to dedicate this thesis to my nine-year-old self who sat watching wolves at the break of dawn in Yellowstone and asked the biologist sitting next to her, “How do I get your job?” Her dream was unwavering, her drive undeniable. My goal that seemed unattainable some days is now within sight. We did it.

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ABSTRACT

Hunting by humans is the primary tool for population control for many ungulate species across the United States, including white-tailed deer (*Odocoileus virginianus*). Previous research has focused primarily on the effects of hunting on prey behavior while neglecting the potential effects hunter behavior has on the probability of harvest success. I examined the influence of hunter movement and habitat use across the landscape on observation rate of white-tailed deer. During the 2008 and 2009 Oklahoma hunting seasons, we recorded GPS and observation data of 83 individual hunters over 487 total hunts. Hunters that moved non-linearly through forested cover at a moderate pace had an increased probability of observing deer. Because deer have been shown to increase use of forested cover and decrease movement during the hunting season, hunters that overlapped habitat use and moved more regularly were more likely to observe deer. Possessing information on what hunter behaviors lead to greater harvest success in an area can be a powerful educational tool for agencies to recruit and retain new hunters, thereby maintaining hunting as a viable management option.

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CHAPTER I

INTRODUCTION

Predator-prey interactions affect ecological processes at the landscape level and affect populations at varying scales from distribution, to changes in vigilance, and foraging patterns (Brown et al. 1999). The landscape of fear is an ecological framework that represents the complex behavioral interactions between predators and prey across a landscape (Laundré et al. 2010). In response to predation risk, prey will alter behavior to decrease risk by changing vigilance and movement behaviors, as well as habitat selection patterns (Brown et al. 1999, Ripple and Beschta 2004, Laundré et al. 2010). Prey exhibit similar and sometimes stronger behavioral responses to predation risk from hunting by humans (hereafter referred to as hunting) as other predators (Proffitt et al. 2009, Cromsigt et al. 2013). Humans are a dominant and influential presence on the landscape (Laliberte and Ripple 2004) and are even the main source of predation and population control for game species in certain areas (Frid and Dill 2002, Marantz et al. 2016). As humans replace large carnivores worldwide, it is important to consider the ecological impacts hunting have on prey species across a landscape (Ripple and Beschta 2004, Little et al. 2014, 2016).

During the hunting season, ungulate prey species become more vigilant and are more likely to flee when there is a perceived risk (Grau and Grau 1980, Frid and Dill 2002, Stankowich 2008, Schuttler et al. 2017). This response is measured by flight initiation distance (FID), which is the distance from a perceived threat that an animal will flee (Grau and Grau 1980). Generally, FID will increase throughout the hunting season as prey become more aware of the perceived predation threat and thus change their behavior (Grau and Grau 1980, Stankowich 2008). FID can be dependent on habitat, season, individual sex and age, level of habituation, history of predation pressure, and level of perceived threat (Grau and Grau 1980, Kufeld et al. 1988, Bender et al. 1999, Stankowich 2008, Reimers et al. 2009, Karns et al. 2012, Schuttler et al. 2017), as well as influenced by non-lethal exposure (Frid and Dill 2002). Ungulate populations show drastic changes in FID from the pre-hunt and scouting periods, increasing through the hunting season, then steadily decrease post-hunt, suggesting that changes in vigilance behavior is relegated to the scouting and hunting season (Millspaugh et al. 2000, Karns et al. 2012, Little et al. 2016, Schuttler et al. 2017).

However, flight behavior can be attention-attracting and energy-cost expensive, thus ungulates may prefer the use of slow, inconspicuous avoidances at longer distances to elude predation (Grau and Grau 1980, Kufeld et al. 1988, Little et al. 2014, 2016). Longer movement patterns increase the vulnerability of the prey in certain habitats given that a moving target is more perceptible and more likely to encounter predators (Swenson 1982, Karns et al. 2012, Little et al. 2014). In these situations, rates of movement decrease during the hunting season (Kilgo et al. 1998, Little et al. 2016, Marantz et al. 2016). Conversely, prey may avoid hunting pressure by moving to and remaining in areas of protection such as urban and suburban areas (Hygnstrom et al. 2011), private properties (Conner et al. 2001, Dzialak et al. 2011, Ranglack et al. 2017), and protected lands (Di Bitetti et al. 2008). Age and sex classes show differences in response as well, with females typically decreasing movement in favor of concealment (Kufeld et al. 1988, Ranglack et al. 2017) while males may maintain home-range sizes at the expense of greater movement and risk (Karns et al. 2012, Marantz et al. 2016).

As hunters are usually limited to hunting during daylight hours, higher rates of diurnal and crepuscular movement increase the vulnerability of individuals while nocturnal movement does not increase vulnerability (Karns et al. 2012). Thus, ungulates may shift to more nocturnal behavior during the hunting season, re-allocating foraging and rutting behavior to the night (Kilgo et al. 1998, Di Bitetti et al. 2008, Bonnot et al. 2013, Little et al. 2016). Differences in habitat type and landscape features are a major factor in changes in prey movement and home-range fidelity (Swenson 1982, Little et al. 2016, Ranglack et al. 2017).

Ungulates also show greater avoidance of roads during hunting seasons, especially during diurnal periods (Kilgo et al. 1998, Millspaugh et al. 2000, Dzialak et al. 2011, Ranglack et al. 2017, O’Connor et al. 2018). During the hunting season, vehicle and foot traffic increases along access roads and the resulting disturbance causes ungulates to avoid these areas (Kilgo et al. 1998, Karns et al. 2012, Paton et al. 2017). However, individual prey with home-ranges containing higher densities of roads may have a higher tolerance and may occupy areas near roads more nocturnally in response to hunting pressure (Dzialak et al. 2011, Wagner et al. 2011). The strength of this response is a function of individual tolerance (Wagner et al. 2011), period of day (Kilgo et al. 1998, Bonnot et al. 2013), surrounding habitat (Kilgo et al.

1998, Karns et al. 2012, Bonnot et al. 2013, Plante et al. 2017), road density (Millspaugh et al. 2000), and level of traffic (Karns et al. 2012, Paton et al. 2017, Plante et al. 2017, Ranglack et al. 2017). Avoidance of roads is a temporary response to hunting pressure and prey may resume occupying roaded areas after the hunting season ends (Kilgo et al. 1998, Millspaugh et al. 2000, Conner et al. 2001, Paton et al. 2017, Plante et al. 2017).

Habitat affects the vulnerability of prey to predation (Laundré et al. 2010, Plante et al. 2017); thus, habitat selection changes during the hunting season (Swenson 1982, Kilgo et al. 1998, Lone et al. 2015). Open habitat increases the likelihood of prey being observed by hunters and thus may increase prey vulnerability (Lebel et al. 2012, Plante et al. 2017). Some ungulates increase selection for areas of greater cover in response to hunting pressure (Kufeld et al. 1988, Kilgo et al. 1998, Millspaugh et al. 2000, Fullman et al. 2017), while some may select for increasingly open habitats with greater visibility within flight distance to cover (Swenson 1982, Stankowich 2008). In areas lacking sufficient vegetative cover, prey may select for varying topography and terrain ruggedness for concealment (Swenson 1982, Paton et al. 2017, Plante et al. 2017), as terrain affects hunter effort and success (Haines et al. 2012, Norum et al. 2015, Plante et al. 2017, O'Connor et al. 2018). Individuals that show increased preference for home-ranges or shift home-ranges to avoid hunting pressure are likely influenced by knowledge of the area, including locations with sufficient cover for hiding and escape routes (Kufeld et al. 1988, Kilgo et al. 1998, Little et al. 2016). Conversely, other individuals may increase their selection of urban and suburban areas, private property, and protected areas to decrease the likelihood of predation (Conner et al. 2001, Hygnstrom et al. 2011, Ranglack et al. 2017). Changes in habitat selection during the hunting season are usually facilitated by available forms of concealment or escape, whether vegetative or topographical, and whether the individual can access cover in their current home range (Swenson 1982, Kufeld et al. 1988, Lone et al. 2015, Ranglack et al. 2017).

Hunter behavior has not been as thoroughly documented and researched as other forms of predator behavior, despite hunting being a major tool for management across the country (Doerr et al. 2001, Harden et al. 2005). White-tailed deer (*Odocoileus virginianus*) populations are increasing throughout their range across the United States (Urbanek et al. 2011). The management of growing populations is a pressing concern among wildlife management agencies and private land owners as increasing urbanization and habitat fragmentation have pushed deer into more conflict with humans (Green et al. 1997, Kilpatrick et al. 2007, Urbanek et al. 2011). Hunting is the main source of population control for white-tailed deer (Harden et al. 2005, Little et al. 2014); thus, understanding what hunter behaviors lead to harvest success increases the effectiveness of hunting as a management tool.

The goal of this research is to quantitatively examine hunter movement, habitat use and prey observations to delineate the relationship between hunter behavior and observation success. I analyzed hunter observation and location data collected by Little (2011) as well as land cover class information (Webb et al., unpublished manuscript) to examine this relationship. I predicted that as hunter movement increased, observation rate would increase; and as habitat cover decreased, observation rate would increase (Chapter 2).

GPS technology has been used to assess and model hunting pressure on a landscape as well as determine small scale effects hunters have on prey behavior (Brøseth and Pedersen 2000). However, no research has examined white-tailed deer hunter behavior at this fine temporal and spatial scale. This study is part of a larger body of research aimed at developing a risk assessment analysis of white-tailed deer across a landscape. Hunters wielding more knowledge of both prey behavior and their own behavior could lead to greater harvest success. As a result, wildlife managers can set harvest goals with greater confidence that these goals will be met during the hunting season. This is especially important for managers concerned with overpopulation, urban wildlife management, or undertaking targeted managed hunts.

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CHAPTER II

EFFECTS OF HUNTER MOVEMENT AND HABITAT USE ON OBSERVATION RATE OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

ABSTRACT

Hunting by humans is the primary tool for population control for many ungulate species across the United States, including white-tailed deer (*Odocoileus virginianus*). Previous research has focused primarily on the effects of hunting on prey behavior while neglecting the potential effects hunter behavior has on the probability of harvest success. I examined the influence of hunter movement and habitat use across the landscape on observation rate of white-tailed deer. During the 2008 and 2009 Oklahoma hunting seasons, we recorded GPS and observation data of 83 individual hunters over 487 total hunts. Hunters that moved non-linearly through forested cover at a moderate pace had an increased probability of observing deer. Because deer have been shown to increase use of forested cover and decrease movement during the hunting season, hunters that overlapped habitat use and moved more regularly were more likely to observe deer. Possessing information on what hunter behaviors lead to greater harvest success in an area can be a powerful educational tool for agencies to recruit and retain new hunters, thereby maintaining hunting as a viable management option.

INTRODUCTION

Hunting by humans (hereafter referred to as hunting) is the primary tool for wildlife population management (Kilpatrick and Walter 1999, Harden et al. 2005, Lebel et al. 2012). Humans are a dominant and influential presence on the landscape (Laliberte and Ripple 2004) and are the main source of predation and population control for game species (Frid and Dill 2002, Marantz et al. 2016). Hunting affects the behavior of white-tailed deer (*Odocoileus virginianus*) on population and landscape levels, leading to concern among management agencies of the potential impacts of hunting (Hygnstrom et al. 2011, Lebel et al. 2012, Little et al. 2014, 2016, Marantz et al. 2016, Schuttler et al. 2017).

Numerous factors and stimuli affect prey behavior in response to predation risk (Frid and Dill 2002), and hunting elicits similar behavioral responses in game species as natural predators (Lebel et al. 2012, Little et al. 2016, Schuttler et al. 2017). In response to human predation risk, prey will change their vigilance, movement behaviors, and habitat selection patterns (Kilgo et al. 1998, Cromsigt et al. 2013, Little et al. 2016, Schuttler et al. 2017). However, the available research detailing behavioral changes of deer in response to hunting often does not account for hunter behavior (Lebel et al. 2012, Little et al. 2014). Before the advent of GPS technology, information on hunter effort and location collected through hunter surveys was open to bias as hunters were required to qualitatively assess and report their own actions. However, GPS technology provides data on hunter behavior in time and space that more accurately depicts hunting pressure across a landscape than previous research methods (Brøseth and Pedersen 2000). This type of data allows for a deeper understanding of what hunter behaviors lead to harvest success.

Harvest success is generally measured by the number of hunters that harvest an animal over the total number of hunters in an area, and hunter effort is measured by the number of prey harvested over the number of hunting days (Grau and Grau 1980, Gratson and Whitman 2000, Kilpatrick et al. 2002, Iijima 2017). Other studies use observation rate as a proxy for harvest, given the assumption that the more animals a hunter observes, the more likely they are to harvest an animal (Jacques et al. 2011, Lebel et al. 2012, Little et al. 2014, 2016). The likelihood of harvest success increases with hunter effort (Murphy 1965) and hunter effort is dependent on access roads and landscape features (Gratson and Whitman 2000, Lebel et al. 2012, Iijima 2017, Ranglack et al. 2017).

Most hunters focus their activity within as little as 100 m of a road or trail (Diefenbach et al. 2005; Lebel et al. 2012). Thus, the probability of harvest generally increases as the amount of access roads increases within hunting areas, dependent on the degree of visibility, traffic and density of roads (Lebel et al. 2012, Paton et al. 2017, Plante et al. 2017, O'Connor et al. 2018). However, ungulates show greater avoidance of roads under predation risk, especially during diurnal periods (Kilgo et al. 1998, Millspaugh et al. 2000, Karns et al. 2012, Bonnot et al. 2013, Paton et al. 2017, Ranglack et al. 2017, O'Connor et al. 2018). Differences also exist between hunting seasons, with stronger avoidance behavior during rifle seasons than archery seasons, which is likely a result of differences in rifle and archery hunter behaviors (Gratson and Whitman 2000, Ranglack et al. 2017).

Landscape features such as slope and habitat type can influence the number of hunting days per harvest (Swenson 1982; Norum et al. 2015; Iijima 2017; O’Connor et al. 2018). Areas with greater visibility may increase harvest success, while varying topography decreases visibility and thus may decrease harvest success (Swenson 1982, Iijima 2017). However, prey change patterns of habitat selection during the hunting season in response to predation pressure (Swenson 1982; Kilgo et al. 1998; Laundré et al. 2010; Lone et al. 2015). These changes are usually facilitated by available forms of concealment or escape, either vegetative or topographical, and whether the individual can access cover in their current home range (Swenson 1982; Kufeld et al. 1988; Kilgo et al. 1998; Lone et al. 2015; Ranglack et al. 2017). Conversely, prey may increase their selection of urban and suburban areas, private property, and protected areas to decrease the likelihood of predation (Conner et al. 2001, Hygnstrom et al. 2011, Ranglack et al. 2017). Given these changes, harvest success may change over the season as deer react to hunting pressure (Lebel et al. 2012, Little et al. 2014, 2016).

The number of deer observed by a hunter during a hunting period may be a result of visibility, deer density, hunter experience, and other variables such as weather (Jacques et al. 2011, Lebel et al. 2012). Hunter experience can have a strong influence on observation rate (Jacques et al. 2011) and may be a good indicator of harvest success (Gratson and Whitman 2000). However, experience does not show the same strong influence in areas with a high density of deer (Lebel et al. 2012). Another strong indicator of success is the degree of visibility; as distance and amount of visual obstruction increases, a hunter is less likely to observe a deer (Jacques et al. 2011, Lebel et al. 2012). Open habitat increases the likelihood of prey being observed by hunters and thus may increase prey vulnerability (Lebel et al. 2012, Plante et al. 2017). In response to hunting pressure, some ungulates increase selection for areas of greater cover (Kufeld et al. 1988; Kilgo et al. 1998; Bonnot et al. 2013; Lone et al. 2015; Ranglack et al. 2017), while some select for more open habitats with greater visibility within flight distance to cover (Swenson 1982, Stankowich 2008). Given that deer increase their use of concealing cover at the onset of the hunting season (Swenson 1982; Kufeld et al. 1988; Kilgo et al. 1998; Paton et al. 2017), visual obstruction can be a determining factor in harvest success (Lone et al. 2015).

The density of prey also influences harvest success (Swenson 1982, Lebel et al. 2012, Plante et al. 2017). As the density of prey increases, the probability of a hunter observing prey or harvest success increases (Hansen et al. 1986, Little et al. 2014, 2016, Iijima 2017). Prey distribution changes over the hunting season as prey become more aware of predation risk and alter movement and behavior (Little et al. 2014). During the hunting season, prey species become more vigilant and are more likely to flee when there is a perceived risk (Frid & Dill 2002; Stankowich 2008; Schuttler et al. 2017).

Flight behavior can be attention-attracting and energy-cost expensive, thus ungulates may prefer the use of slow, inconspicuous avoidance of hunters at longer distances to elude predation (Grau & Grau 1980; Little et al. 2014; Little et al. 2016). Longer movement patterns increase the vulnerability of the prey in certain habitats given that a moving target is more perceptible and more likely to encounter predators (Swenson 1982; Little et al. 2014). In these situations, rates of movement decrease and home range fidelity increases (Little et al. 2016; Marantz et al. 2016). Additionally, prey may avoid hunting pressure by moving to and remaining in areas of protection such as urban and suburban areas (Hygnstrom et al. 2011), private properties (Conner et al. 2001; Ranglack et al. 2017), and protected lands (Di Bitetti et al. 2008). Age and sex classes show differences in response as well, where females typically decrease movement in favor of concealment (Kufeld et al. 1988, Ranglack et al. 2017) while males maintain home-range sizes at the expense of greater movement and risk (Karns et al. 2012, Marantz et al. 2016). As hunters are usually limited to hunting during daylight hours, higher rates of diurnal and crepuscular movement increase the vulnerability of individuals, while nocturnal movement does not increase vulnerability (Karns et al. 2012). Thus, ungulates may shift to more nocturnal behavior during the hunting season, re-allocating foraging and rutting behavior to the night (Di Bitetti et al. 2008, Reimers et al. 2009, Bonnot et al. 2013, Little et al. 2016). Differences in habitat type and landscape features are a major factor in changes in prey movement and home-range fidelity (Swenson 1982, Kilgo et al. 1998, Bonnot et al. 2013, Little et al. 2014, 2016, Fullman et al. 2017, Ranglack et al. 2017).

Hunter effort and observation rate are usually dependent on road access, landscape features, visibility, prey densities, and experience (Jacques et al. 2011; Lebel et al. 2012; Norum et al. 2015; Ranglack et al. 2017; O’Connor et al. 2018).

However, prey alter their vigilance behaviors, movement patterns, and habitat selection (Kufeld et al. 1988; Kilgo et al. 1998; Conner et al. 2001; Stankowich 2008; Bonnot et al. 2013; Little et al. 2016; Marantz et al. 2016) which directly interacts with hunter behaviors and effects harvest success. The changes in behavior exhibited by prey are often limited to pre-hunt scouting and hunting seasons with normal behavior resuming after the hunting season ends, suggesting that human hunting pressure is a major source of predation risk to game populations and elicits notable responses (Kilgo et al. 1998, Conner et al. 2001, Marantz et al. 2016, Paton et al. 2017).

Hunting is an activity based long in tradition, with methods and locations passed down through the generations (Gratson and Whitman 2000). While prey alter their behavior in response to hunting, it should follow that hunters adjust their behavior in response to prey. Understanding what behaviors affect harvest success may increase hunter efficiency and effectiveness. Considering that hunting is a both a major source of revenue as well as the primary tool for population control (Doerr et al. 2001, Harden et al. 2005), managers can utilize information of successful hunter behaviors to manage populations across the landscape by manipulating where and how hunting pressure influences prey (Cromsigt et al. 2013). Controlled hunts have been shown to be successful for management of overabundant urban and suburban deer populations (Green et al. 1997, Kilpatrick et al. 1997, 2002, Kilpatrick and Walter 1999). Urban and suburban environments limit hunters in where and when to hunt; thus, qualitatively defining where hunter behavior overlaps with deer behavior would create a more targeted approach to hunting by identifying specific hunter behaviors and hunter habitat selection that lead to greater harvest success. As white-tailed deer populations continue to grow across the United States (Urbanek et al. 2011), the ability to develop targeted management plans to control populations swiftly and effectively is increasingly vital (Green et al. 1997, Kilpatrick et al. 2007, Urbanek et al. 2011).

In this study, I examine human hunter movement and habitat use to determine which behaviors have the most significant effect on observation rate of white-tailed deer. Additionally, I examine hunter resource selection across the landscape at the population level. This study is part of a larger body of research regarding hunter and white-tailed deer predator-prey interactions.

STUDY AREA

The Noble Research Institute's Oswalt Road Ranch (ORR) is located in Love County, Oklahoma, USA (Figure 1). It is a 1,861-ha ranch within the Cross Timbers and Prairie eco-region consisting of mixed wooded areas, bottomlands, uplands and rangeland (Gee et al. 2011). The average road density was 1.4 km/km^2 of paved, gravel and dirt roads at the time of the study (Webb et al. 2020 unpublished manuscript). Elevation ranges from 233 to 300 m, and slope ranges from 0 to 41 degrees (Webb et al. 2020 unpublished manuscript). During the 2008 and 2009 study periods, rainfall was 0.07 cm in 2008 and 0.2 cm in 2009; average daily temperature was 6.48° in 2008 and 7.51° C in 2009 (Burneyville, OK; Oklahoma Mesonet; www.mesonet.org). For a full description of the study area, see Little (2011).

METHODS

During the study period, the ranch was non-operational and did not graze cattle or perform prescribed burnings. No hunting was permitted on the property for >1.5 years preceding to the study period to minimize carry-over effects of previous hunting exposure. Prior to 2007, lease hunting on the property permitted $\bar{x} = 5$ hunters. Little (2011) collected GPS and survey information from all hunters during the 2008 and 2009 white-tailed deer rifle seasons. Hunters were not allowed to harvest collared deer to avoid reduction of sample size. The property allotted the harvest of 20 antlerless deer each year, with 3 mature, un-collared antlered deer in 2008, and 4 mature, un-collared antlered deer in 2009.

Hunter Assignment and Observations

The ORR was divided into 3 treatment areas based on existing landscape features, property boundaries, and fencing to produce 3 areas of similar sizes and vegetation composition (Little 2011). These areas consisted of no hunting pressure (control), low hunting pressure (1 hunter/101 ha), and high hunting pressure (1 hunter/30 ha). In 2008, the control area totaled 679 ha in size, high hunting pressure totaled 583 ha, and the low hunting pressure totaled 586 ha (Figure 2). To create temporal replication, the treatment areas were randomly reassigned pressures, resulting in a clockwise shift for the 2009 hunting season (Figure 3). Treatment areas were divided into hunting compartments to maintain the proper hunter/ha density for the different hunting pressures. The high hunting pressure treatment area was divided into 19 compartments in 2008 and 21 compartments in 2009, while the low hunting pressure treatment area was divided into 6 compartments both years. Individual hunters were assigned to one hunting compartment for that hunting period. For more information, see Little (2011).

Hunters were required to spend ≥4 hours/day/compartment during the weekend when participation was highest. At all times, hunters carried a Garmin Extrex Venture GPS unit (Garmin, Olathe KS) to track their locations with a fix attempt every minute (recorded in datum NAD83, UTM Zone 14N, accuracy ±10 m). To remove locations not associated with hunting behavior, GPS location points were truncated to coincide with legal shooting hours and within assigned hunting compartments. Hunters were required to record the start and end times of their activities within the assigned hunting compartment each day, the number of deer observed within the compartment (number of collared antlered deer, and number of un-collared antlered and antlerless deer), and hunting method used (e.g. tree-stand, ground-blind, still, or specified other).

Landscape Classification

The Noble Research Institute developed a vegetation type and land use map combined with a digital elevation model (DEM) (Webb et al., unpublished manuscript). Digital raster layers were re-sampled using a 1 m resolution grid into a 17 m resolution grid following the 2009 growing-season National Agriculture Imagery Program (NAIP; USDA Farm Service Agency, Salt Lake City, UT) aerial imagery and using ERDAS Imagine 9.3 software (ERDAS, Inc, Atlanta, GA) (Little 2011). The reclassification of the 17 m resolution was based on fractal analysis

(Webb et al. 2009) to coincide with the smallest patch size perceived by deer and because most location errors were ≤ 3.7 m (Webb et al., unpublished manuscript). Three vegetative cover types were classified based on vegetative structure of the study area: forest, mixed forest/ shrubland/ grassland (mixed), and grassland (Webb et al., unpublished manuscript). Forested areas were classified as having greater than 70% closed canopy cover, grassland areas as greater than 70% open canopy, and mixed areas as having less than 70% of both closed and open canopy (Webb et al., unpublished manuscript). Little (2011) used supervised classification based on spectral signatures, zonal majority and majority fraction features to classify each 17 m pixel into either forest, mixed, or grassland vegetative types. Roads, anthropogenic features, and water features were masked during the supervised classification to prevent misclassification (Little 2011). The 17 m resolution grid was then reclassified to 30 m resolution to match the resolution of other existing data layers with the addition of riparian vegetation type by buffering streams by 50 m (Webb et al., unpublished manuscript). Roads (paved, gravel and dirt), water sources (ponds), and anthropogenic features (barns, houses, well pads, etc.) were heads-up digitized as vector layers, then converted to raster, and added into the vegetation classification map (Webb et al., unpublished manuscript). The resulting raster layer (NAD83, UTM Zone 14N, 30 m resolution) contained information for the following classes: forest, mixed, grassland, road, riparian, pond, anthropogenic feature, and barren ground (Figure 4).

Data Analysis

Movement Covariates

Movement is a function of trajectory and velocity over time; in telemetry data, these factors are often represented by discrete steps, displacement vectors, and time in relation to physical position (Smouse et al. 2010, Hooten and Johnson 2017). To quantitatively represent differences in hunter movement behavior, I used Program R packages ‘trajr’ (McLean and Skowron Volponi 2018), ‘adehabitatLT’ (Calenge 2006), and ‘recurse’ (Bracis et al. 2018) to calculate movement parameters based on GPS location data for each hunt record. These movement parameters were divided into two suites of movement behavior for analysis: movement and path shape. To represent hunter movement, I calculated step length, net squared displacement, and residence time for each record. Step length was the length (m) between two consecutive points in a trajectory (McLean and Skowron Volponi 2018). Because of the regular 1 min fixes, step length can be considered a measurement of velocity (m/min). Net squared displacement (m^2) was the square of the Euclidean distance between one point in the trajectory and the origin of the movement path (Bastille-Rousseau et al. 2015). Residence time was the total time spent (minutes) within a defined radius of the previous point in a trajectory, where the radius equaled the maximum standard GPS fix error (10 m + 3.6 standard error; Bracis et al. 2018). Additionally, I calculated residence time as a proportion of the total time spent hunting to adjust for variation, as hunts could vary greatly in total time spent afield. To represent path shape, I calculated the turning angle and sinuosity of each record.

Turning angle was the direction (radians) in which the hunter traveled between consecutive points in a trajectory (McLean and Skowron Volponi 2018). This was an absolute value to highlight the severity of the turn rather than the direction. Sinuosity was calculated using the standard deviation of the turning angle divided by the square root of the step length and is an index from 0-1 representing the straightness of a trajectory, where 0 is straight and 1 is highly curved (Bovet and Benhamou 1988; Table 1). For each movement parameter, except sinuosity as it is a scaled index, I calculated summary statistics for each hunt including the following values: minimum, median, maximum, mean, standard deviation, variation, and coefficient of variation.

Habitat Use Covariates

Using both continuous and discrete data, hunter habitat use was divided into two suites: proportion of time spent in vegetation cover classes and the mean use of landscape features. Vegetation cover classes were represented using the landcover raster layer classes for forest, mixed, grassland, and riparian cover (Figure 4, see above). I extracted raster cell values from GPS points for each hunt record using the ‘raster’ package in Program R (Hijmans et al. 2014). Habitat use was calculated by dividing the sum of each cell value count for each vegetation cover class by the total number of GPS points in each record to create a value representing the proportion of locations spent in a vegetation cover class during a single hunt.

Use of landscape features was represented using distance to features and the roughness data layers created in ArcGIS 10.6.1 (ArcGIS$^{®}$ software by Esri). I performed a reclassification of the landcover raster layer where each cell in the new raster layers was given a value based on the Euclidean distance from the specified feature. This included distance to anthropogenic features, ponds, and roads. Because there is less than 100 m of variation in elevation on ORR, I use roughness to represent variation in topography. The scale at which hunters perceive the landscape can be considered the average shooting distance for the study area, which is 100-150 m (Springer 1977). Thus, to create the roughness layer, I used a 30 m resolution Digital Elevation Model (DEM) raster layer and performed a zonal reclassification using a 10x10 roving window to represent the shooting window (300 m x 300 m) where the standard deviation of the elevation was assigned to the focal cell. I then extracted raster cell values from GPS points for each hunt record using the 'raster' package in Program R (Hijmans et al. 2014) and took the mean value for distance to anthropogenic features, ponds, and roads, and the mean landscape roughness for each hunt record (Table 2).

Statistical Analysis

Multilevel modeling provides individual-based information on behaviors and links relationships between hunter habitat use, movement patterns, and observation rate of deer (Gillies et al. 2006, Dzialak et al. 2011, Wagner et al. 2011). To analyze the relative importance of covariates, I used a multilevel modeling approach to reduce the number of competing models (Franklin et al. 2000). Covariates measuring related behavioral parameters were separated into suites, which included: movement, path shape, vegetation cover class, and landscape features. I removed any covariates that were correlated ($|r| \geq 0.7$) based on Pearson's correlation coefficient (Ranglack et al.

2017). I standardized all covariates by subtracting the mean and dividing by 2 times the standard deviation (Gelman 2008, Lele 2009). I evaluated multiple functional forms (linear, quadratic, and pseudothreshold) for each covariate as the relationship to observation rate could be nonlinear. Pseudothreshold functional forms were fit using a natural log transformation (Franklin et al. 2000).

The first level of model selection for hunter behavior involved taking the individual behavioral suites and fitting univariate models for each covariate and functional form against the observation rate of white-tailed deer (deer observed per hour hunting) in competing models. To do this, I used a Gaussian distribution in a generalized linear model (GLM) using the ‘lme4’ package in Program R (Bates et al. 2015). I then ranked the models using Akaike’s Information Criterion (AIC) (Akaike 2011) and moved all covariates within 2 ∆AIC units to the next level of models (Ranglack et al. 2017). The second level model selection combined the top covariate forms within each suite to determine which covariate best represented movement and habitat use according to AIC. The final level model combined the best performing models to represent both hunter movement and habitat use behavior.

Numerous behavioral factors influence whether a hunter harvests an animal that can be difficult to quantify and analyze. Thus, I used observation rate as a proxy for harvest success under the assumption that the more deer a hunter observed, the more likely a hunter is to successfully harvest. To confirm the relationship between observation and harvest success, I performed binomial logistic regression analyses on the total number of deer observed and observation rate against harvest success (Little et al. 2014). Additionally, compartment availability of vegetation cover classes could have influenced hunter habitat use more strongly than hunter behavior. Thus, to determine if hunters were using vegetation cover classes in higher proportions to availability, I performed GLMs using a Gaussian distribution comparing hunter use and compartment availability (Gillies et al. 2006).

Population Level Resource Selection

A resource selection function (RSF) is a statistical model that analyzes the selection of resources by an individual (Boyce et al. 2002, Manly et al. 2002). Individual selection is typically modeled as presence vs. absence, or presence vs. available in cases when absence is assumed, within units of selection (i.e. pixels of land) that represent resources and associated predictor variables (e.g. elevation, slope, or habitat) (Boyce et al. 2002, Manly et al. 2002). RSFs provide the probability of use of a resource unit based on the observed use or non-used of the unit (Boyce et al. 2002, Manly et al. 2002).

To represent hunter resource selection at the population level, I examined all hunt records together. As hunters were assigned to specific compartments for the duration of the hunt, I represented availability by creating one point per raster cell within the assigned compartment. Hunter presence was represented by the GPS location data. Resources available for use included vegetation cover classes and landscape features. I represented habitat covariates at the spatial scale at which hunters perceive the landscape, considered to be the average shooting distance of 150 m (Springer 1977). Using the landcover raster layer (Figure 4), I performed a zonal reclassification where each raster cell was classified to one of the landcover classes (e.g. forest, mixed, grassland, road, riparian, pond, anthropogenic feature, and barren ground). The focal cell was valued as the count of cells of a specified class within a 10x10 roving window, which I then took as the percent of the shooting window. For distance covariates, I performed a reclassification based on Euclidean distance where each cell in the new raster layers was given a new value based on the distance from the specified feature. Landscape variation was once again represented using the standard deviation of elevation (see above). Raster cell values were extracted to each point using the package ‘raster’ in Program R (Hijmans et al. 2014) (Table 3).

The multilevel modeling process (see above) was replicated for the population level RSF with only two levels of model selection. I separated covariates into two suites: vegetation cover class and landscape features. The first level model selection fit univariate models for each hunter presence covariate and functional form in the two suites against resource availability in competing GLMs using a binomial distribution. Including individual hunter as a random effect did not improve model fit ($\Delta AIC_c = 400510.5$); therefore, data was pooled by record and not by individual. Models were ranked using AIC and all covariates within 2 ΔAIC_c units were moved to the next level of models (Ranglack et al. 2017). The second level model selection combined the top covariate forms into a single model to represent hunter resource selection.

RESULTS

During the 2008 and 2009 hunting seasons, deer observation and location data from 83 hunters for 516 individual records of a single hunt by a hunter in the assigned compartment were collected. Over 140,000 total GPS location points were collected. Between the two hunting seasons, 29 animals were harvested by hunters (2008: 1 male, 10 females. 2009: 4 males, 14 females). Of the 516 records collected for this study, 29 were removed from analysis with associated errors for a total of 487 records used for all analyses. Of the over 140,000 individual GPS fixes collected for this study, 111,706 were used for the analyses.

Hunters spent on average 3.73 hours (SE = 0.08), traveled 2,085 m (SE = 79.04), and observed 2.73 deer per individual hunt (SE = 0.15). Between each GPS fix (1 fix per minute), the mean step length per hunt record averaged at 9.4 m (SE = 0.3). The mean absolute turning angle of hunters per hunt averaged 0.27 radians (SE = 0.01). The mean proportion of residence time averaged 46% of the hunt spent within 10 m ± 3.6 SE m of the previous GPS location. The proportion of use of different vegetation cover classes per hunt times averaged as follows: 16% forested cover, 22% mixed cover, and 38% grassland cover, and 24% riparian cover. The mean roughness used per hunt averaged 5.78 (SD of elevation, SE = 0.1) (Table 4).

The probability of harvest increases as the total number of deer observed increases ($p < 0.01$, SE = 0.04, $z = 4.398$), and as observation rate increases ($p < 0.01$, SE = 0.14, $z = 3.916$) (Figure 8). Hunters showed a stronger preference for forested cover in proportion to availability than other vegetation cover classes ($p < 0.01$, SE =

0.10, t = 3.227) (Figure 9). No other significant functional responses were observed (Figure 9).

Model Selection

From the GLMs using a Gaussian distribution, the best covariates for each movement suite and functional form included linear mean step length, mean turning angle as a quadratic function, and mean residence time as a quadratic function (Table 5). There were two models within 2 ΔAIC_c units of the top model for hunter movement, therefore the most parsimonious model was selected. This model involved linear mean step length and mean turning angle as a quadratic function. The best covariates for each habitat use suite and functional form included linear proportion of use for grasslands, forests, mixed, and mean roughness (Table 6). Distance covariates did not show a significant effect on observation rate. There were five models within 2 ΔAIC_c units of the top model for hunter habitat use (Appendix C), therefore the most parsimonious model was selected, containing only the proportion of forested cover use. The top combined model for hunter movement and habitat use included all of the best competing covariates: linear mean step length, mean turning angle as a quadratic function, and linear proportion of hunt spent in forested cover (Table 7). As average step length increases, the model predicts the number of deer observed per hour will increase (standardized coefficient estimate ± SE; 0.3 ± 0.09; Figure 6). The predicted number of deer observed is the lowest when the mean absolute turning angle is approximately 0.3 radians with predicted observations increasing as the mean absolute turning angle increases or approaches 0 (0.06 ± 0.1; Figure 6). As the mean proportion of hunt time spend within forested cover increases, the number of deer observed per hour increases (0.42 ± 0.09; Figure 6).

From the RSF logistic regression models, the best competing functional forms for each covariate included: distance to ponds and roads as pseudothresholds, linear distance to anthropogenic features, forest and riparian cover as quadratic functions, mixed cover as a pseudothreshold, and roughness as a pseudothreshold (Table 8). The most supported model included each of the covariates (model weight = 1), with the next highest model within 41.21 ΔAIC_c units. Predicted use of forested cover is highest at 40% forested habitat within the shooting window (Figure 7). Predicted use of mixed cover quickly increases before plateauing at 5% mixed cover within the shooting window (Figure 7). Predicted use of riparian cover is lowest at 50% riparian cover within the shooting window, with use increasing as availability either increases or approaches 0% (Figure 7). Predicted use decreases as distance to ponds increases, quickly plateauing in predicted use after approximately 200 m of distance (Figure 7). Predicted use increases as distance to roads increases, quickly reaching its threshold at approximately 50 m of distance (Figure 7). Predicted use increases as roughness increases, and distance to anthropogenic features increases (Figure 7).

DISCUSSION

Most research has focused on the effect of hunting pressure on prey behavior while little research has analyzed hunter behavior with a focus on behavior leading to harvest success. Hunter behavior, in terms of how movement and habitat use influences observation of deer, has not been previously measured on such a fine temporal and spatial scale. My results suggest that hunter movement and habitat use have an effect on the number of deer observed during a hunt. Hunters that used forested cover in higher proportions of their hunt were more likely to observe deer than hunters that used forested cover in lower proportions. Additionally, hunters selected for mixed cover more reliably than forested cover based on availability. Hunters that that had higher rates of movement were more likely to observe deer than hunters with lower rates of movement. Walking at approximately 25 m/min (1 mph), the model predicts hunters will observe 1 deer per hour. During movement, hunters that either did not turn or turned more sharply were more likely to observe deer than hunters that turned more moderately. Hunters that turned 0.8 radians per minute were predicted to observe 2 deer per hour, while hunters that only turned 0.3 radians per minute were predicted to observe less than 1 deer per hour.

Previous research has determined hunter effort and observation rate are usually dependent on road access, landscape features, visibility, prey densities, and experience (Jacques et al. 2011; Lebel et al. 2012; Norum et al. 2015; Ranglack et al. 2017; O'Connor et al. 2018), while prey alter their vigilance behaviors, movement patterns, and habitat selection (Kufeld et al. 1988; Kilgo et al. 1998; Conner et al. 2001; Stankowich 2008; Bonnot et al. 2013; Little et al. 2016; Marantz et al. 2016). During the study period, deer avoided hunting pressure by increasing selection for forested cover, decreasing diurnal movement, and increasing site fidelity (Little 2011). Deer increased use of forested cover by 1.7-2.5 times and mixed cover by 1.4-2.3 times in response to predation pressure (Little 2011). Collared deer that were unobserved by hunters moved 38.3% less than observed collared deer, suggesting that greater movement increased observability (Little 2011). Thus, as hunter use of forested cover and movement increased, hunters were more likely to observe deer as deer use of forested cover increased and movement decreased.

The increased probability of observing deer within forested habitat supports increased prey densities as an indicator of harvest success (Hansen et al. 1986, Little et al. 2014, 2016, Iijima 2017). Deer increase use of security areas and cover to avoid predation pressure (Kufeld et al. 1988; Kilgo et al. 1998; Bonnot et al. 2013; Lone et al. 2015; Ranglack et al. 2017), which was supported by the 1.7-2.5 times increase in forested cover use by deer observed by Little (2011). Furthermore, the increased probability of observing deer as mean step length and mean absolute turning angle increased may be a result of triggering flight behavior in deer. Prey perceive higher rates of movement and more direct trajectories as more threatening and trigger flight behavior (Grau & Grau 1980). As flight behavior is attention-attracting, deer that had greater movement during the hunting period were considered more observable (Little 2011). Thus, as deer increase use of forested cover and decrease movement, hunters that increase use of forested cover and increase movement are more likely to observe a deer by overlapping habitat use and potentially triggering a flight response (Grau & Grau 1980; Little et al. 2014; Little et al. 2016).

However, these results contradict studies that have showed increased visibility to be a main indicator of harvest success (Swenson 1982, Jacques et al. 2011, Lebel et al. 2012, Plante et al. 2017). On ORR, visual obstruction increased from grasslands to forests (Little 2011), which should indicate a decrease in observation rate for hunters that used more forested cover. The RSF determined the predicted use of forested habitat was highest at 40% forested habitat within the shooting window of 150 m with decreased predicted use as availability increased, while predicted use of mixed habitat plateaued after 5% mixed habitat within the shooting window (Figure 6). This suggests that hunters were more likely to select for mixed habitat as available more reliably than forested habitat. Mixed habitat had less visual obstruction than forested habitat, which may account for the selection of larger areas of mixed habitat, but this selection did not significantly affect observation rate. Deer altered their habitat use and movement behaviors following the initial 3-day exposure to predation pressure and selected more strongly for forested habitat than mixed habitat (Little 2011), suggesting that once deer are aware of predation pressure, overlapping habitat use becomes a more important factor in determining observation success than visibility.

Access roads have been shown to be a large influence on the number of hunting days per harvest with hunters selecting for shorter distances from roads (Kilgo et al. 1998, Ranglack et al. 2017), which our data did not reflect. The RSF determined predicted use increased as distance to roads increased (Figure 6). However, this relationship did not show a significant effect on observation rate. ORR did not have substantive internal road systems for hunters to utilize during their hunts. Compartment boundaries were often marked by pathways and simple, two-track roads, which limited hunter use as well. Additionally, the truncation of movement to be within assigned compartments removed nearly all use of roads by eliminating transit to and from the compartment. While roads may be a significant source of hunter decision on other properties and within other studies (Kilgo et al. 1998, Gratson and Whitman 2000, Ranglack et al. 2017), the layout of ORR and the study design largely eliminated use of roads by hunters; thus, I did not find a significant effect on observation rate. Hunters also showed a strong preference in their selection of areas with higher roughness (Figure 6), which aligns with literature suggesting varying topography to be an indicator of success (Swenson 1982, Iijima 2017). However, the low variation of the topography of the study area led to no significant effect of roughness of observation rate of deer. Given that the elevation of the study area ranged from 233-300 m and the slope averaged 4.12 degrees (SE = 0.02) (Webb et al., unpublished manuscript), habitat composition had a greater effect on visibility than topography in terms of observation rate.

The positive relationship between number of deer observed and harvest success supports our use of observation rate as a proxy to harvest success and our assumption that as observation rate increases, likelihood of harvest increases (Figure 7). For the 2008 and 2009 hunting seasons, ORR had a harvest quota of 20 antlerless deer each year, with 3 mature, un-collared antlered deer in 2008, and 4 mature, un-collared antlered deer in 2009. This limited harvest on the property while observations were unlimited. Only 29 harvests occurred of the study period while 1333 deer were observed, leading to the relationship being highly variable. Further research with higher rates of harvest success would be necessary to more confidently determine the strength of this relationship and what additional hunter behaviors may not only lead to increased observation rate, but harvest success as well.

It is important to note that hunters participating in this study were limited in their decision-making options regarding behavioral choices. As this study was originally designed to control for hunting pressure across a landscape by assigning hunters to compartments (Little 2011), hunters were limited to what was available to them within the compartment. Compartments could vary greatly in habitat composition and landscape features (Appendix A and B). Coupled with the truncation of GPS location points, this could account for the sharp threshold reached in predicted use as distance to ponds and roads increased, as well as the negative linear relationship of distance to anthropogenic features in the RSF. The available riparian cover ranged from 0-73% with an average of 22% of the compartment composition. Despite the high variability of available riparian habitat, predicted use of riparian cover only varied from 0.33-0.38 (Figure 7), suggesting hunters did not select strongly for riparian areas and this selection did not have a significant effect on observation rate. The available forested cover ranged from 0-45% with an average of 18% of the compartment composition; however, hunters used forested cover in higher proportions to compartment availability (Figure 9). Given that use of forested habitat was one of the most important covariates in predicting the number of deer observed, hunters that had limited availability of forested cover at their disposal during their hunts did not necessarily observe less deer because of active behavioral decisions, but rather because of predetermined compartment assignments.

Predator-prey relationships are important ecological functions and, as hunting by humans is a primary tool for deer management, human hunting behavior should be considered and researched in the same detail as other species (Harden et al. 2005, Lebel et al. 2012, Cromsigt et al. 2013). Future research should seek to collect hunter movement and observation data with the same level of spatial detail without limiting hunters to specific compartments to better understand hunter behavior when allowed full autonomy of decision-making. More temporal information on observation data would also increase understanding of what particular behaviors at a moment in time might have led to an observation, rather than a general summary of all behaviors during a hunt.

MANAGEMENT IMPLICATIONS

White-tailed deer populations are increasing throughout their range across the United States (Urbanek et al. 2011) and increasing urbanization and habitat fragmentation has pushed deer into more conflict with humans (Green et al. 1997, Kilpatrick et al. 2007, Urbanek et al. 2011). There is an increasing need to improve hunting as a management tool to more effectively manage growing populations (Cromsigt et al. 2013). By identifying and optimizing where hunter and prey behaviors interact, managers have the potential to create more targeted approaches to hunting and population management. The ability to determine what behaviors and areas maximize the probability of harvest, for example movement through forested cover, increases the efficiency and effectiveness of hunting as a tool. In the case of urban and suburban deer management where management must consider how to remove a specific number of animals from an area with limited time and space availability (Hansen and Beringer 1997, Kilpatrick and Walter 1999, Kilpatrick et al. 2002, 2007), the ability to maximize probability of behavioral overlaps between deer and hunters would increase the efficiency of a targeted hunt. Conversely, if the goal of management is to increase prey populations by decreasing harvest success, identifying what hunter behaviors lead to greater harvest success would delineate methods to decrease the level of predator-prey interactions. Limiting the overlaps of habitat use by increasing road closures or adjusting hunting areas would likely decrease hunter success by limiting where hunter behaviors and prey behaviors overlap (Kilgo et al. 1998, Ranglack et al. 2017).

One issue currently facing management agencies is the low recruitment and retention of hunters (Ryan and Shaw 2011). Hunting is an activity based long in tradition, with methods and locations passed down through the generations (Gratson and Whitman 2000). Often, knowledge can be a barrier to new hunters in an area (Ryan and Shaw 2011). Thus, possessing information on what hunter behaviors lead to greater harvest success in an area can be a powerful educational tool for agencies to recruit and retain new hunters, thereby maintaining hunting as a viable management option.

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FIGURES AND TABLES

Table 1: Covariates included in the hunter movement analysis. Values derived from hunter GPS location data.

Covariate	Unit	Description
Step Length	meters	the length between two consecutive points in a trajectory
Turning Angle	radians	absolute value of direction traveled between consecutive points in a trajectory
Sinuosity	index (0-1)	the standard deviation of the turning angle/the square root of the step length
Net Squared Displacement	meters	the square of the Euclidean distance between one point in the trajectory and the origin of the movement path
Residence Time	proportion of hunt	locations within 10 m + 3.6 SE of the previous point in a trajectory/total locations

Table 2: Covariates included in the hunter habitat use analysis. Values derived from raster layer.

Covariate	Unit	Description
Forest	proportion of hunt	locations within habitat with >70% closed canopy/total locations
Grassland	proportion of hunt	locations within habitat with >70% open canopy/total locations
Mixed	proportion of hunt	locations within habitat with <70% open or closed canopy/total locations
Riparian	proportion of hunt	locations within 50 m buffer of streams/total locations
Anthropogenic Features	meters	Euclidean distance from anthropogenic features (barns, houses, well pads, etc.)
Roads	meters	Euclidean distance from roads (paved, gravel, and dirt)
Ponds	meters	Euclidean distance from water sources (e.g. ponds)
Roughness	SD of elevation	Zonal reclassified layer using 10x10 window to take the standard deviation of elevation from 30 m DEM

Table 3: Covariates included in the population level resource selection analysis. Values derived from raster layer.

Covariate	Unit	Description
Forest	% shooting window	Zonal reclassified layer of the 30 m resolution landcover class layer using 10x10 window to take count of cells with >70% closed canopy
Mixed	% shooting window	Zonal reclassified layer of the 30 m resolution landcover class layer using 10x10 window to take count of cells with <70% closed canopy
Riparian	% shooting window	Zonal reclassified layer of the 30 m resolution landcover class layer using 10x10 window to take count of cells within 50 m buffer of streams
Anthropogenic Features	meters	Euclidean distance from anthropogenic features (barns, houses, well pads, etc.) using the 30 m resolution landcover class layer
Roads	meters	Euclidean distance from roads (paved, gravel, and dirt) using the 30 m resolution landcover class layer
Ponds	meters	Euclidean distance from water sources (e.g. ponds) using the 30 m resolution landcover class layer
Roughness	SD of elevation	Zonal reclassified layer using 10x10 window to take the standard deviation of elevation from 30 m DEM

Table 4: Summary statistics for most significant variables based on each hunt record.

Variable	Mean	Std. Error
Total Observations (# of deer)	2.74	0.15
Total Time (hours)	3.73	0.08
Total Distance (m)	2085	79
Mean Step Length (m/min)	9.41	0.30
Mean Turning Angle (radians)	0.27	0.01
Residence Time (proportion of hunt)	0.46	0.01
Forest Use (proportion of hunt)	0.16	0.01
Mixed Use (proportion of hunt)	0.22	0.01
Grassland Use (proportion of hunt)	0.37	0.02
Mean Roughness (SD of elevation)	5.77	0.10

Table 5: Standardized coefficient estimates, standard errors, p-values, and t-values for the GLM using a Gaussian distribution of the top movement model.

Covariate	Estimate	Standard Error	p-value	t-value
Intercept	0.58	0.07	<0.01	8.24
mean step length	0.35	0.14	0.01	2.55
mean turning angle	0.06	0.10	0.54	0.62
(mean turning angle)^2	0.31	0.12	<0.01	2.66
mean residence time	0.01	0.14	0.95	0.06
(mean residence time) ^{2}	0.52	0.20	<0.01	2.59

Table 6: Standardized coefficient estimates, standard errors, p-values and t-values for the GLM using a Gaussian distribution of the habitat use model.

Covariate	Estimate	Standard Error	p-value	t-value
Intercept	0.79	0.04	<0.01	17.91
proportion of field use	-0.04	0.1	0.67	-0.42
proportion of forest use	0.4	0.1	<0.01	3.79
proportion of mixed use	0.06	0.1	0.56	0.59
mean roughness	0.11	0.09	0.24	1.17

Table 7: Standardized coefficient estimates, standard errors, p-values, and t-values for the GLM using a Gaussian distribution of the top full movement and habitat use model.

Covariate	Estimate	Standard Error	p-value	t-value
Intercept	0.70	0.05	<0.01	13.54
mean step length	0.30	0.09	<0.01	3.16
mean turning angle	0.06	0.1	0.51	0.65
(mean turning angle)^2	0.34	0.1	<0.01	3.01
proportion of forest use	0.42	0.09	<0.01	4.83

Table 8: Standardized coefficient estimates, standard errors, p-values, and z-values for the logistic regression of the top resource selection model.

Covariate	Estimate	Standard Error	p-value	z-value
Intercept	-0.78	0.01	<0.01	-119.96
distance to anthropogenic features	-0.12	0.01	<0.01	-8.72
log(distance to ponds)	-0.22	0.01	<0.01	-32.99
log(distance to roads)	0.26	0.01	<0.01	26.13
forested habitat	0.31	0.01	<0.01	26.99
(forested habitat)^2	-0.31	0.01	<0.01	-21.96
log(mixed habitat)	0.43	0.01	<0.01	43.58
riparian habitat	-0.16	0.01	<0.01	-16.61
(riparian habitat)^2	0.11	0.02	<0.01	5.97
log(roughness)	0.34	0.01	<0.01	34.50

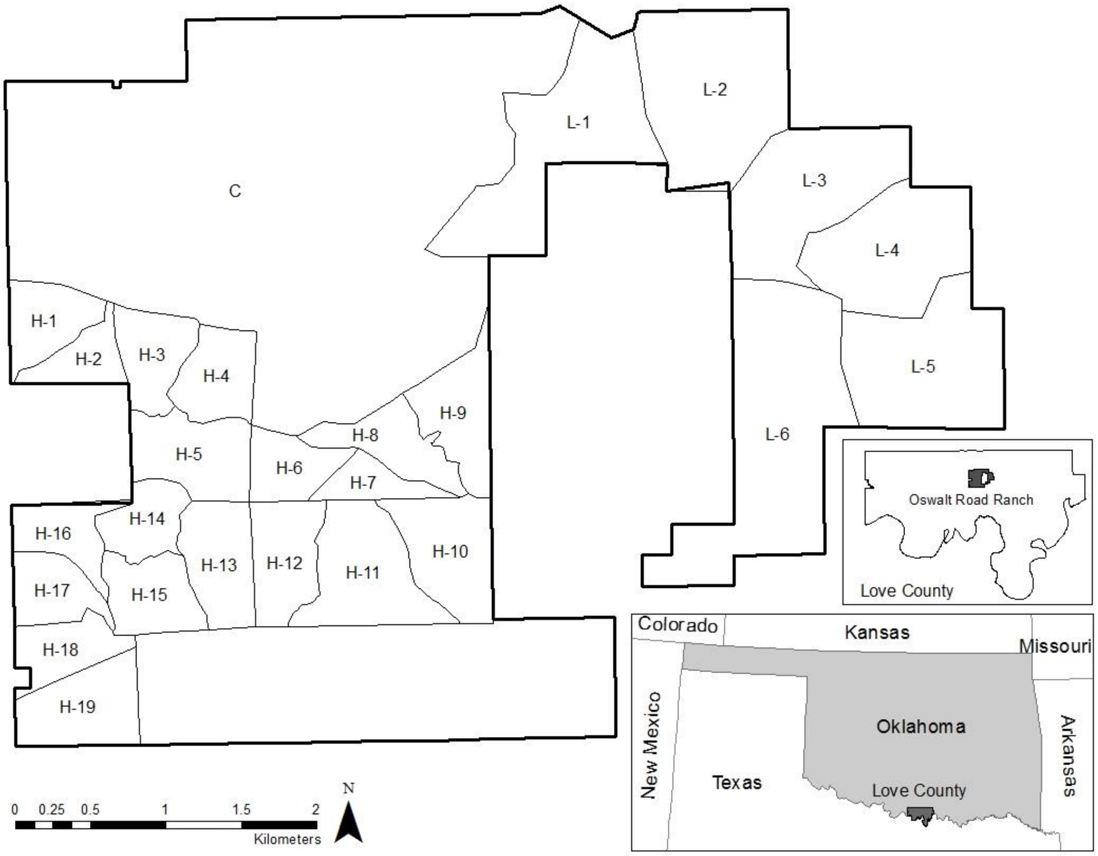

Figure 1: The Noble Research Institute's Oswalt Road Ranch located in Love County, Oklahoma, USA with 2008 treatment compartments delineated. Map produced in ArcGIS 10.6.1 (ArcGIS® software by Esri).

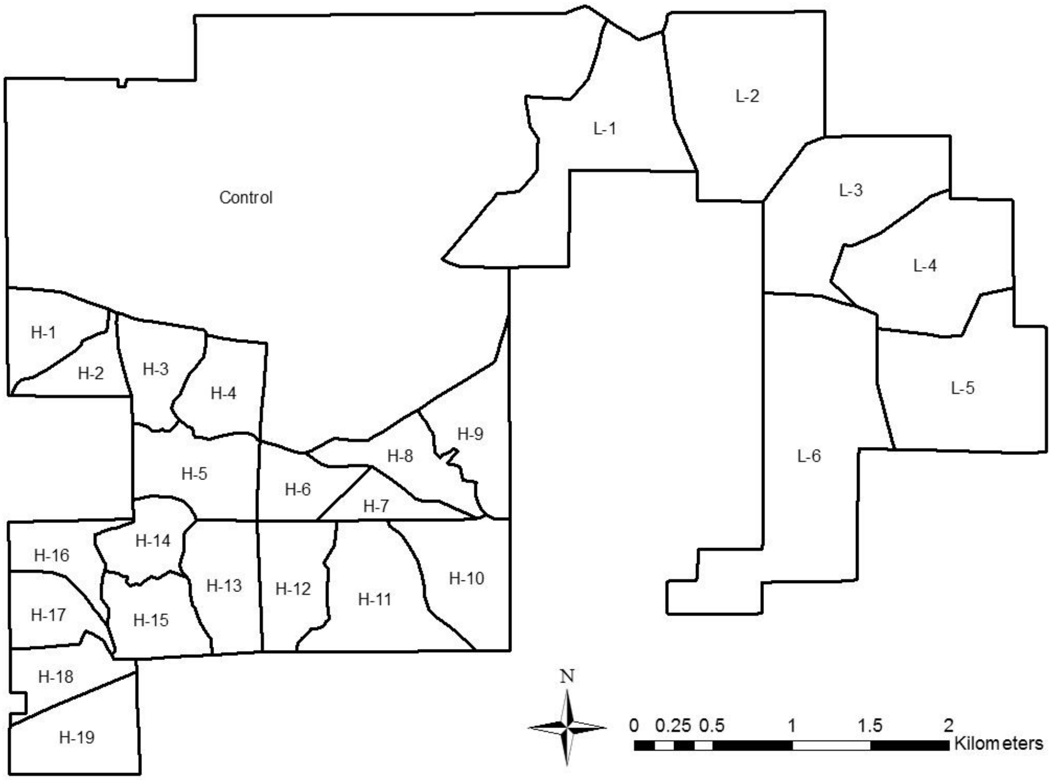

Figure 2: Treatment compartments for the 2008 hunting season on the Noble Research Institute's Oswalt Road Ranch where control (C) = no hunters on 679 ha; low-risk (L) = 1 hunter/101 ha on 585 ha total; and high-risk (H) = 1 hunter/30 ha on 583 ha total. Compartments were shifted clockwise for the 2009 hunting season (Figure 3). Map produced in ArcGIS 10.6.1 (ArcGIS® software by Esri).

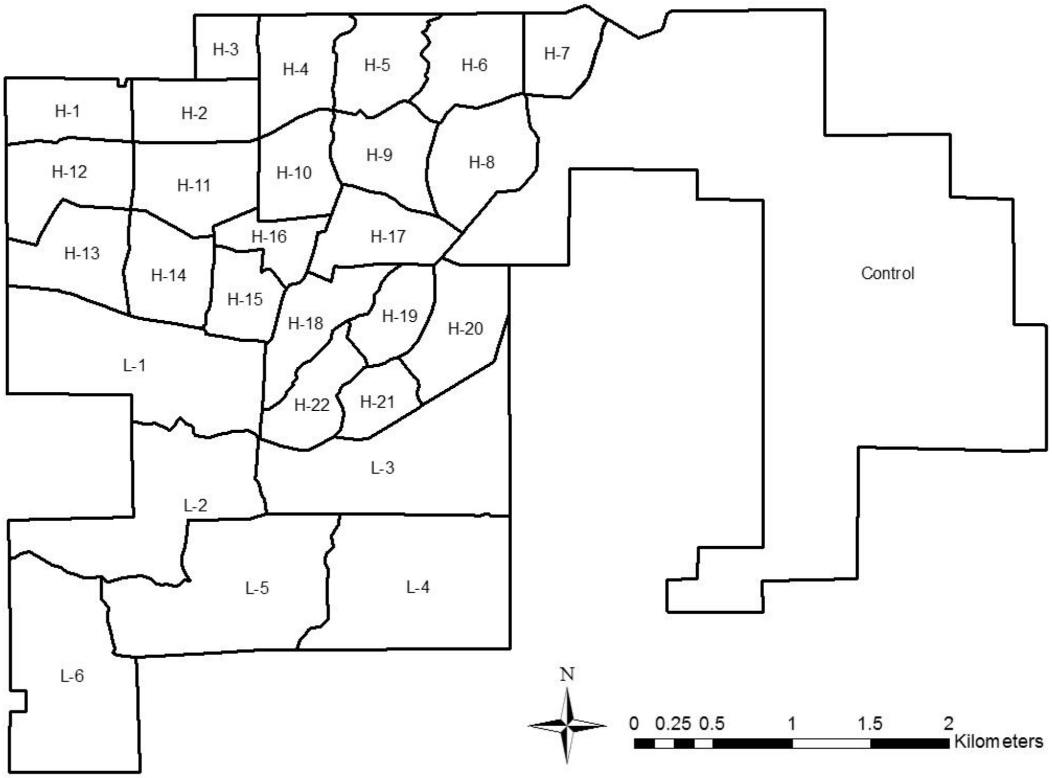

Figure 3: Treatment compartments for the 2009 hunting season on the Noble Research Institute's Oswalt Road Ranch where control (C) = no hunters on 586 ha; low-risk (L) = 1 hunter/101 ha on 583 ha total; and high-risk (H) = 1 hunter/30 ha on 679 ha total. Map produced in ArcGIS 10.6.1 (ArcGIS® software by Esri).

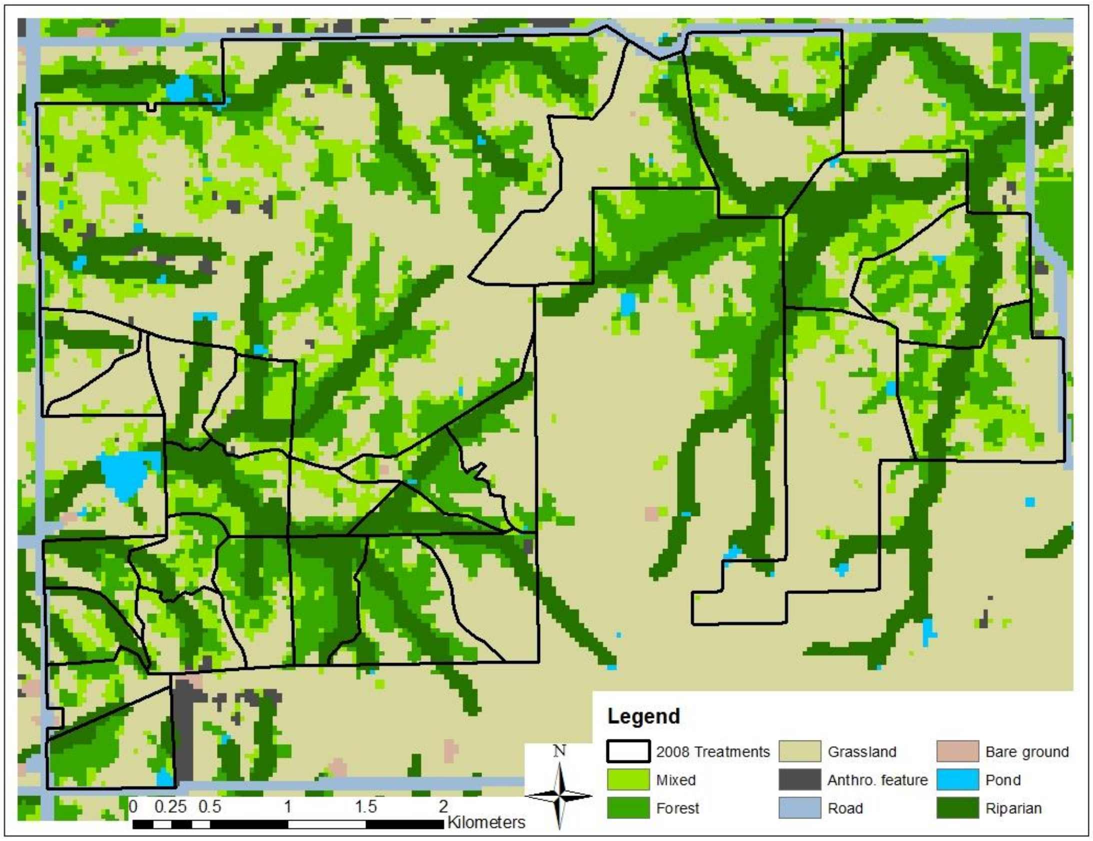

Figure 4: Land cover class raster layer of the Noble Research Institute's Oswalt Road Ranch with associated classes: forest, mixed, grassland, riparian, pond, road (paved, gravel, dirt), anthropogenic features (barns, houses, well pads, etc.), and barren ground. Map produced in ArcGIS 10.6.1 (ArcGIS® software by Esri).

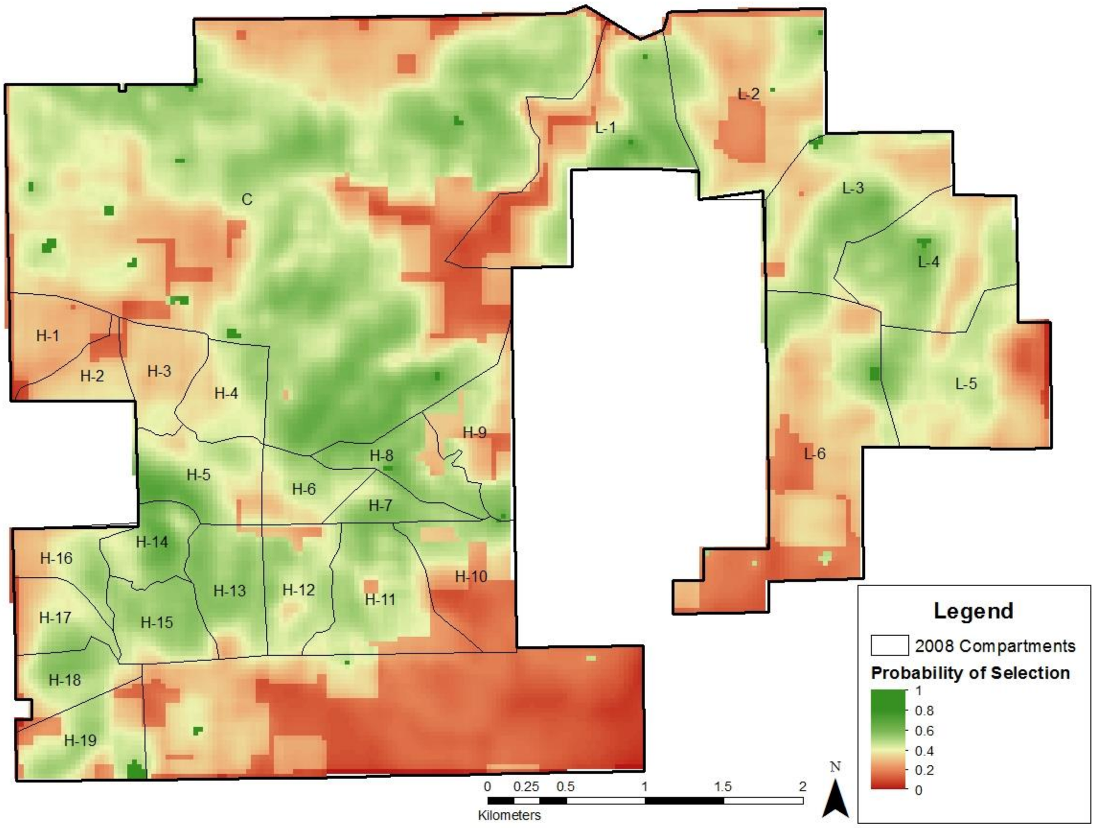

Figure 5: Predicted probability of hunter selection on the Noble Research Institute's Oswalt Road Ranch with 2008 hunting compartments represented. Map produced in ArcGIS 10.6.1 (ArcGIS® software by Esri).

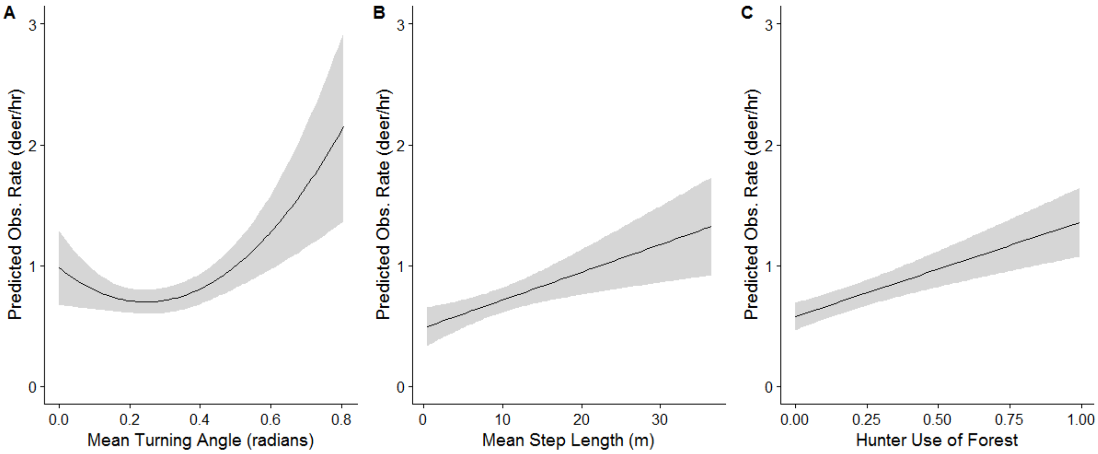

Figure 6: Plots of three covariates included in the top model of hunter movement, habitat use and observation rate of white-tailed deer. (A) Mean turning angle (radians); (B) mean step length (m); (C) proportion of use of forested habitat.

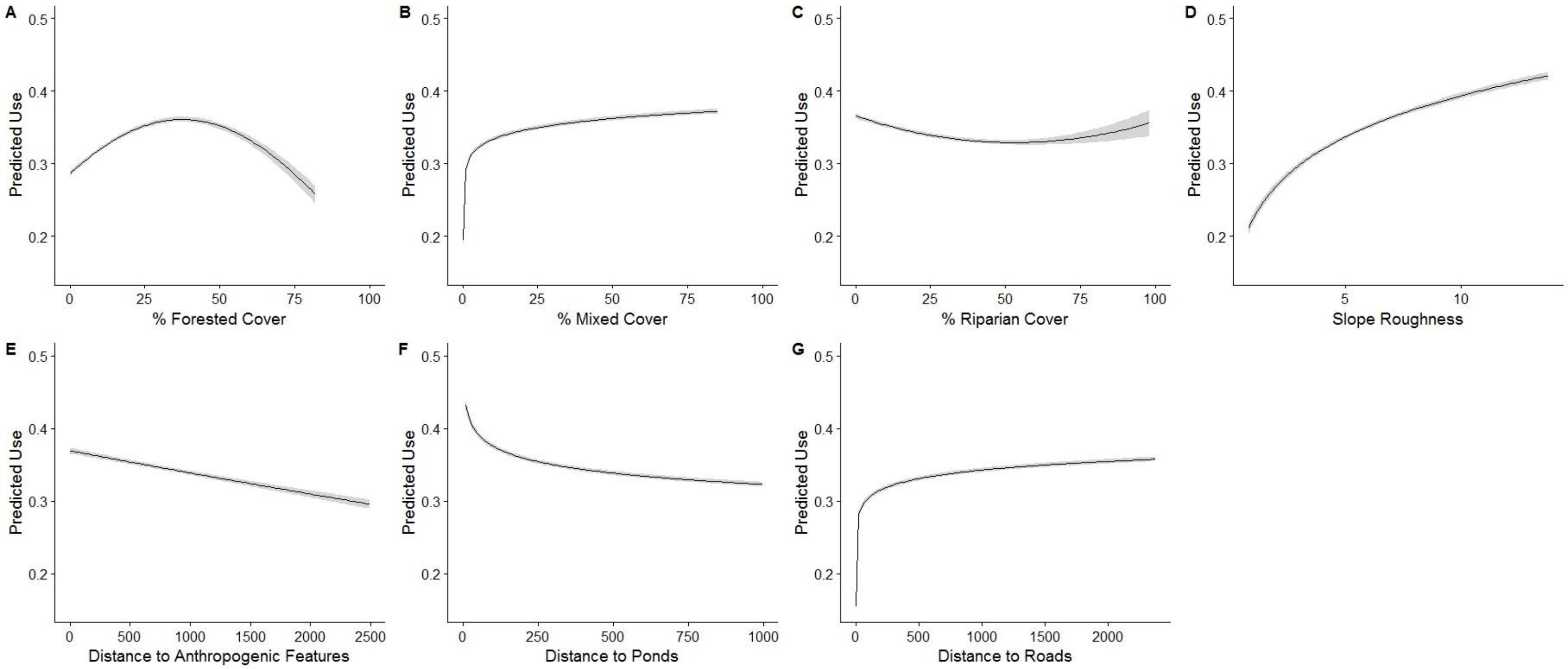

Figure 7: Plots of seven covariates included in the top model of population level resource selection of white-tailed deer hunters. (A) Percent forested cover of shooting window; (B) percent mixed cover of shooting window; (C) percent riparian cover of shooting window; (D) available roughness (SD of elevation); (E) available distance to anthropogenic features (m); (F) available distance to ponds (m); (G) available distance to roads (m).

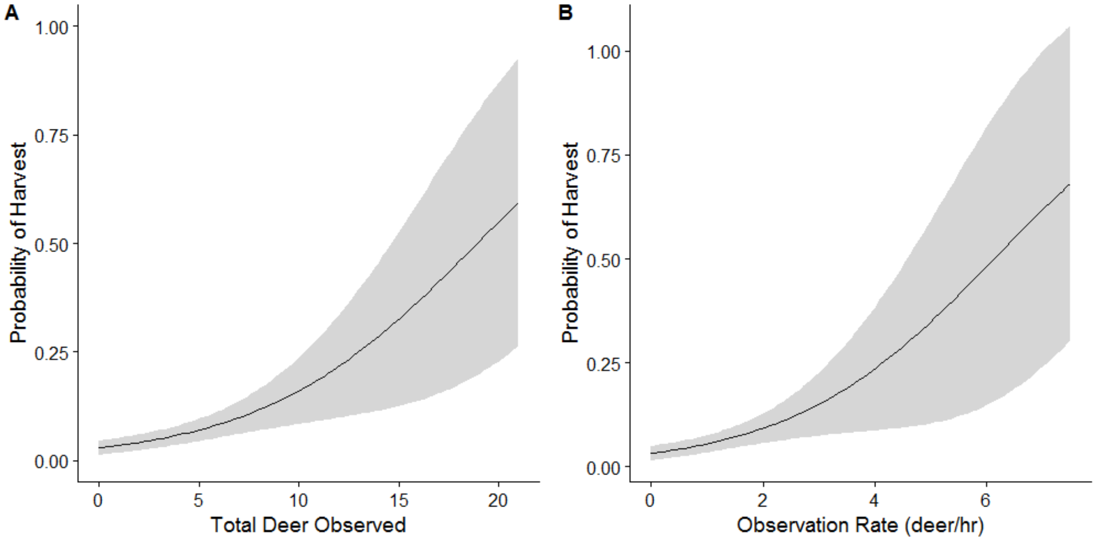

Figure 8: Plots of binomial logistic regression models of white-tailed deer harvest by hunters. (A) Total deer observed during a hunt (# of deer); (B) Observation rate (# of deer/hour).

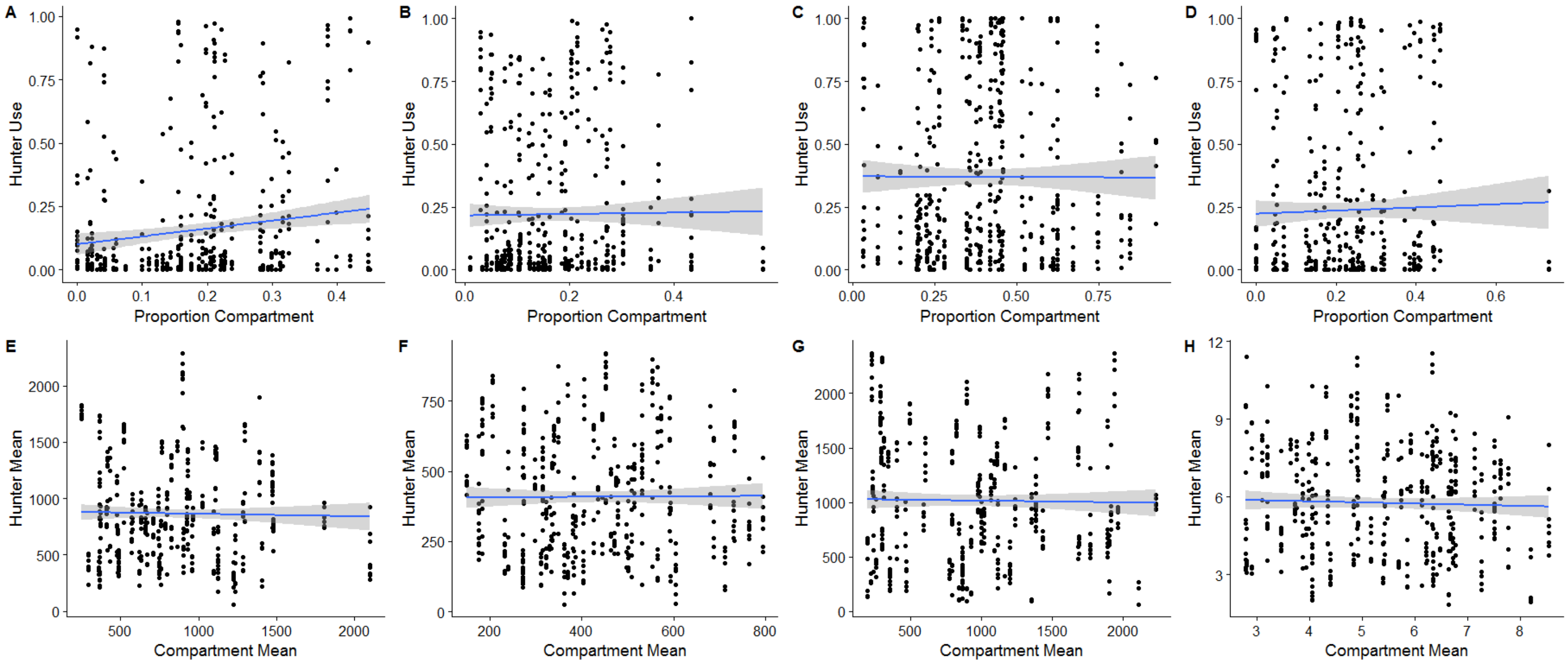

Figure 9: Plots of generalized linear models using a Gaussian distribution of hunter use versus compartment availability. (A) Proportion of hunter use of forested habitat over proportion of forested habitat available within a compartment; (B) Proportion of hunter use of mixed habitat over proportion of mixed habitat available within a compartment; (C) Proportion of hunter use of grassland habitat over proportion of grassland habitat available within a compartment; (D) Proportion of hunter use of riparian habitat over proportion of riparian habitat available within a compartment; (E) Mean hunter distance from

anthropogenic features (m) over mean compartment distance from anthropogenic features (m); (F) Mean hunter distance from ponds (m) over mean compartment distance from ponds (m); (G) Mean hunter distance from roads (m) over mean compartment distance from roads (m); (H) Mean hunter roughness (SD of elevation) over mean compartment roughness (SD of elevation).

APPENDIX A: 2008 Compartment composition summary

Habitat composition and landscape features for the 2008 compartments on the Oswalt Road Ranch.

Compartment	Total Area (ha)	% Forest	% Grassland	% Mixed	% Riparian	Mean Distance to Roads (m)	Mean Distance to Ponds (m)	Mean Distance to Anthropogenic Features (m)	Mean Roughness (SD of elevation)
H1	26.91	3.01	52.17	10.37	23.75	223.44	475.31	939.14	2.90
H2	18.81	0.00	92.34	7.66	0.00	462.92	404.77	862.32	2.91
H3	27.72	2.27	62.34	4.87	29.87	927.76	311.93	1095.56	4.06
H4	29.16	7.41	23.46	26.23	41.05	1352.76	362.07	931.40	4.40
H5	39.33	19.22	7.55	27.23	46.00	1109.77	471.77	823.86	5.85
H6	23.58	9.92	41.98	35.50	12.60	1681.16	552.98	413.72	3.88
H7	15.84	13.07	3.41	10.23	73.30	1690.06	272.73	370.54	6.73
H8	28.98	41.93	24.53	13.98	17.70	1936.73	240.32	364.08	5.75
H9	36	15.50	60.25	3.25	20.75	2110.12	330.86	783.62	3.93
H10	44.46	14.37	67.00	1.01	16.19	1237.29	436.16	827.57	4.12
H11	54.18	38.54	27.74	6.98	26.74	1090.66	452.72	705.64	6.32
H12	34.56	44.79	3.13	7.55	44.53	1199.22	590.89	746.84	6.68
H13	35.64	36.87	33.33	14.90	14.90	1118.10	764.08	627.98	7.26
H14	23.22	29.84	19.38	30.23	20.54	793.27	508.01	660.40	8.53
H15	30.15	13.73	34.63	28.36	20.60	822.46	686.92	294.74	7.77
H16	22.5	20.40	24.00	13.20	38.40	297.09	402.66	362.44	4.85
H17	24.39	5.54	23.25	18.45	44.28	236.46	730.02	430.46	6.22
H18	24.75	22.18	44.36	14.91	13.09	301.14	711.89	247.72	6.69
H19	38.97	30.48	41.80	5.08	17.32	232.56	383.57	367.23	5.16
L1	97.11	11.03	74.42	8.34	4.63	793.20	380.24	577.72	3.77

L2	101.34	5.95	44.23	19.09	25.31	468.39	299.18	618.35	3.98
L3	81.27	15.50	19.71	23.59	40.64	1018.57	425.31	1296.35	5.48
L4	72.99	22.56	35.64	20.47	20.84	606.36	323.28	1806.33	6.21
L5	87.03	23.78	38.16	22.34	13.44	492.72	497.04	2102.66	4.91
L6	143.01	4.15	81.81	8.31	4.72	1384.71	349.06	1233.99	3.10

APPENDIX B: 2009 Compartment composition summary

Habitat composition and landscape features for the 2009 compartments on the Oswalt Road Ranch.

Compartment	Total Area (ha)	% Forest	% Grassland	% Mixed	% Riparian	Mean Distance to Roads (m)	Mean Distance to Ponds (m)	Mean Distance to Anthropogenic Features (m)	Mean Roughness (SD of elevation)
H1	31.59	15.95	22.51	56.98	0.00	342.82	322.27	411.56	3.73
H2	31.95	28.17	26.20	36.90	7.61	591.06	205.76	764.47	4.31
H3	16.29	9.94	45.30	10.50	26.52	196.08	271.21	743.67	4.05
H4	34.83	3.10	43.41	13.95	32.04	314.03	604.56	1109.14	5.40
H5	32.94	1.91	44.81	8.74	39.62	293.11	564.09	1114.59	5.43
H6	36.81	19.80	20.05	16.14	39.61	288.23	316.02	926.97	6.77
H7	24.93	28.52	26.35	19.86	18.05	229.78	501.73	475.58	6.64
H8	41.85	31.18	45.59	8.82	13.76	894.20	335.47	957.34	6.41
H9	34.02	29.37	45.50	10.32	14.81	869.52	531.68	1475.04	7.50
H10	30.96	20.93	57.56	21.51	0.00	978.23	731.21	1481.16	7.62
H11	39.96	1.58	62.16	27.03	4.28	998.40	274.07	1125.89	4.90
H12	39.51	2.28	38.50	43.28	6.83	355.98	184.83	485.28	3.21
H13	38.16	4.25	35.38	19.10	31.37	402.47	175.73	798.49	3.46
H14	33.93	0.00	61.01	6.10	25.46	987.37	150.80	1285.94	2.79
H15	23.13	17.51	41.63	12.45	26.07	1466.96	232.34	1221.54	4.05
H16	18.99	39.81	45.50	7.11	7.58	1432.61	593.11	1408.18	6.48
H17	34.38	15.97	74.61	4.19	5.24	1384.16	793.88	1388.01	4.34
H18	33.39	31.54	20.49	30.19	16.98	1766.44	513.93	899.22	6.12
H19	22.59	18.73	51.39	10.36	19.52	1890.96	478.12	903.41	6.34
H20	39.06	12.21	84.33	3.00	0.00	1961.29	369.18	1022.80	2.81

H21	18.99	45.02	34.60	20.38	0.00	2233.78	333.80	366.99	5.70
H22	27.00	22.00	25.67	27.67	24.67	1904.04	565.06	478.70	8.19
L1	101.70	3.54	54.25	12.92	25.75	777.93	387.20	965.27	3.64
L2	82.98	22.67	14.43	24.95	37.09	844.10	464.02	667.30	6.34
L3	100.71	21.09	38.96	15.19	24.13	1912.88	339.97	521.49	4.78
L4	99.99	28.08	44.73	4.14	22.41	1165.46	444.81	755.80	5.41
L5	99.72	32.49	22.20	15.34	29.15	1068.49	679.49	570.16	7.13
L6	93.42	20.62	37.57	12.24	23.51	258.59	571.83	356.41	5.91

APPENDIX C: Model selection of habitat use

Model selection of the top 5 of 16 models within 2 ΔAICc for observation rate of white-tailed deer across proportion of habitat use for forested, grassland, mixed cover classes and roughness.

Model	df	logLik	ΔAIC_c	weight
deer/hour ~ forest	3	-674.82	0.00	0.26
deer/hour ~ forest + roughness	4	-674.08	0.55	0.19
deer/hour ~ forest + mixed	4	-674.43	1.25	0.14
deer/hour ~ forest + grassland	4	-674.53	1.45	0.12
deer/hour ~ forest + mixed + roughness	5	-673.72	1.89	0.10

CHAPTER III

SYNTHESIS AND RECOMMENDATIONS

Predator-prey relationships are complex behavioral interactions that are an integral ecological process, affecting populations at the landscape level (Brown et al. 1999). Humans are a dominant and influential presence on the landscape (Laliberte and Ripple 2004) and are even the main source of predation and population control for game species such as white-tailed deer (*Odocoileus virginianus*) (Frid and Dill 2002, Harden et al. 2005, Marantz et al. 2016). However, hunter behavior has not been as thoroughly documented and researched as prey behavior, despite hunting by humans (hereafter referred to as hunting) being a major tool for management across the country (Doerr et al. 2001, Harden et al. 2005). As hunters are considered part of the predator-prey relationship with white-tailed deer (Cromsigt et al. 2013), it is important to understand what behaviors lead to greater harvest success to not only better understand prey behavior, but better develop hunting as a management tool as well.

GPS technology has been used to assess and model hunting pressure on a landscape as well as determine small scale effects hunters have on prey behavior (Brøseth and Pedersen 2000). However, no research has examined white-tailed deer hunter behavior in terms of movement and habitat use at this fine temporal and spatial scale. My results determined that there is a positive relationship between the number of deer observed and the probability of harvest success, confirming our assumption that observation rate was an appropriate proxy to harvest success. Moreover, hunters that move at a moderate pace, non-linearly through forested cover are more likely to observe white-tailed deer. As deer will increase use of forested habitat and decreases movement in response to predation pressure (Little et al. 2014, 2016), my results suggest that the overlap of hunter and deer behavior is an integral part of observation success. Thus, to increase the effectiveness of hunting as a management tool, it is important to understand not only prey behavior, but hunter behavior as well.

These results contradict studies that have found visibility to be an indicator of harvest success (Swenson 1982, Jacques et al. 2011, Lebel et al. 2012, Plante et al. 2017), but corroborates studies that have found prey densities to be indicator of success (Hansen et al. 1986, Little et al. 2014, 2016, Iijima 2017). In my study area, visual obstruction increased from grasslands to forests (Little 2011), which should indicate a decrease in observation rate for hunters that used more forested habitat. However, deer altered their habitat use and movement behaviors following the initial 3-day exposure to predation pressure (Little 2011), suggesting that once deer are aware of predation pressure, overlapping habitat use becomes a more important factor in determining observation rate than visibility. Similarly, previous research has found that access roads have a large influence on hunter effort (Kilgo et al. 1998, Gratson and Whitman 2000, Ranglack et al. 2017), which was not reflected in my results.

The discrepancies in my results and other findings may be a result of the habitat composition of the study area. Oswalt Road Ranch had limited availability of landscape features and habitat that have been shown to influence harvest success. Thus, future research should seek to collect hunter movement and observation data with the same level of spatial detail without limiting hunters to specific compartments and in varying habitat types to better understand hunter behavior when allowed full autonomy of decision-making. More temporal information on observation data would also increase understanding of what particular behaviors at a moment in time might have led to an observation, rather than a general summary of all behaviors during a hunt. Furthermore, the relationship between harvest success and observation rate was limited in my study due to the low numbers of harvest over the study period. Gathering further data with either higher rates of harvest or over a longer study period would more definitively illuminate the relationship between hunter behavior and harvest success.

White-tailed deer populations are increasing throughout their range across the United States (Urbanek et al. 2011) and increasing urbanization and habitat fragmentation has pushed deer into more conflict with humans (Green et al. 1997, Kilpatrick et al. 2007, Urbanek et al. 2011). There is an increasing need to improve hunting as a management tool to more effectively manage growing populations (Cromsigt et al. 2013). By identifying and optimizing where hunter and prey behaviors interact, managers have the potential to create more targeted approaches to hunting and population management. In the case of urban and suburban deer management where management must consider how to remove a specific number of animals from an area with limited time and space availability (Hansen and Beringer 1997, Kilpatrick and Walter 1999, Kilpatrick et al. 2002, 2007), the ability to maximize probability of behavioral overlaps between deer and hunters would increase the efficiency of a targeted hunt. Conversely, if the goal of management is to increase prey populations by decreasing harvest success, identifying what hunter behaviors lead to greater harvest success would delineate methods to decrease the level of predator-prey interactions. Limiting the overlaps of habitat use by increasing road closures or adjusting hunting areas would likely decrease hunter success by limited where hunter behaviors and prey behaviors overlap (Kilgo et al. 1998, Ranglack et al. 2017).

One issue currently facing management agencies is the low recruitment and retention of hunters (Ryan and Shaw 2011). Hunting is an activity based long in tradition, with methods and locations passed down through the generations (Gratson and Whitman 2000). Often, knowledge can be a barrier to new hunters in an area (Ryan and Shaw 2011). My results predict that a hunter moving through forested cover at approximately 1 mph and turning less than a quarter turn every minute is predicted to observe >1 deer per hour of hunt. Additionally, hunters that observe more deer are more likely to successfully harvest an animal. Providing similar information to hunters based on the area and prey species can be a powerful educational tool for agencies to recruit and retain new hunters, thereby maintaining hunting as a viable management option.

Predator-prey relationships are important ecological functions and, as hunting by humans is a primary tool for deer management, human hunting behavior should be considered and researched in the same detail as other species (Harden et al. 2005, Lebel et al. 2012, Cromsigt et al. 2013). My results provide a template for what hunter behaviors lead to greater observation rate, and thereby greater harvest success that can be expanded by further research into different study areas. Hunters wielding more knowledge of both prey behavior and their own behavior could lead to greater harvest success and managers can utilize information of successful hunter behaviors to manage populations across the landscape by manipulating where and how hunting pressure influences prey (Cromsigt et al. 2013). As a result, wildlife managers can set harvest goals with greater confidence that these goals will be met during the hunting season. This is especially important for managers concerned with overpopulation, urban wildlife management, or undertaking targeted managed hunts.

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