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Using spatial methods to analyse anthropogenic predation risk and movement ecology of white-tailed deer (*Odocoileus virginianus*)

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Geography

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Using spatial methods to analyse anthropogenic predation risk and movement ecology of white-tailed deer (*Odocoileus virginianus*)

Abstract

Hunting has been used as a central tool by wildlife managers to maintain populations of game species, however, we still lack a good understanding of exactly how hunting influences deer biology. Technological advances in GPS data over the last two decades now enable us to perform more detailed analysis on the effects of human hunters on wildlife populations. This research explores the spatial ecology of hunters and White-tailed deer in the Cross Timbers ecoregion of Oklahoma. Using new statistical methodologies to analyse simultaneous GPS tracking data on deer and hunters to study their spatial interactions. The results show how new methods allow us to quantify the spatial ecology and behaviour of White-tailed deer in response to predation pressure from human hunters in combination with the biotic and abiotic drivers of predation risk and flight response. Giving wildlife managers greater understanding to influence deer populations, and landscapes, in the future.

Keywords

Ecology, cervids, *Odocoileus virginianus*, hunting, GIS, wildlife management.

Summary for Lay Audience

White-tailed deer are an important species economically, culturally, and biologically across the Americas. They are the most widely distributed deer species ranging from South America all the way up to the Yukon Territory and spanning the continent from the eastern seaboard to British Columbia. This species exerts pressure on plant communities, including forestry plantations and has bottom-up effects on predator populations that depend on them for food. Although White-tailed deer declined steeply following the arrival of Europeans, they have now rebounded to historically high levels due to the

success of the North American Model of Wildlife Conservation (NAM). While this is a conservation success, high numbers of deer can lead to human-wildlife conflict where they are over abundant and cause damage such as loss to forestry or wildlife-vehicle collisions.

Hunting has been used as a central part of the NAM to manage game species since its creation in the early 1900s. Population management relies on a tag-based system and hunters harvest deer from the population in numbers that are sustainable. Yet, deer numbers remain above carrying capacity (the number of individuals the landscape can sustain) across many ecoregions. This presents complex challenges for wildlife managers who need to balance the costs and benefits of deer for multiple stakeholder groups. Although this species is well studied from a hunter perspective, regarding hunter success and trophy size, less is known about the impacts of hunters on deer behaviour and space use on the landscape. It is known that fear and stress can have direct impacts on deer population numbers, as can the forage availability the deer are able to access. Therefore, it would benefit managers to understand how hunting impacts deer behaviour and the subsequent ways this information can be harnessed to better reach our management goals.

This research seeks to test new methodologies to gain a greater understanding of the relationship between hunters and deer and how this influences deer behaviour and landscape use. Harnessing this information will allow managers to better understand the impacts of hunting on deer populations and achieve their management goals.

Co-Authorship Statement

Research collaborator Dr. Stephen Webb of Noble Research Institute, Ardmore, Oklahoma, United States provided the deer GPS tracking data for both 2008 and 2009 hunting seasons from the Oswalt Road Ranch. Stephen Webb also provided all information related to the trapping, sedation and collaring of deer. Additionally, Dr. Webb provided habitat raster's and hunting treatment information from work completed with Dr. Andrew Little in previous years. Assistance with coding and statistical analysis was provided by Dr. Jed Long and Dr. Simon Bonner.

“You may write me down in history
With your bitter, twisted lies,
You may trod me in the very dirt
But still, like dust, I’ll rise.

Does my sassiness upset you?
Why are you beset with gloom?
Cause I walk like I’ve got oil wells
Pumping in my living room.

Just like moons and like suns,
With the certainty of tides,
Just like hopes springing high,
Still I’ll rise.

Did you want to see me broken?
Bowed head and lowered eyes?
Shoulders falling down like teardrops,
Weakened by my soulful cries?

You may shoot me with your words,
You may cut me with your eyes,
You may kill me with your hatefulness,
But still, like air, I’ll rise...

Bringing the gifts that my ancestors gave,
I am the dream and the hope of the slave.

I rise

I rise

I rise.”

– Maya Angelou

This thesis is dedicated to all those who came before me and persevered so that I may prosper today. I am my ancestors' wildest dreams.

My grandfather Bernard, who will not get the opportunity to see me finish this degree like I thought he would. I hope I have made you proud.

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List of abbreviations and definitions

Contact = the co-occurrence of two individuals in the same location, at the same time based on assigned spatial and temporal thresholds.

CWD = Chronic Wasting Disease

Displacement = distance between starting location and end location.

Edge habitat = Environments along the edge of distinct habitat types which can result in edge effects.

Edge species = Species that prefer the mixed habitat on the boundary between different ecosystems.

Fitness = The ability of an individual to pass on their genes and produce offspring.

Fitness is dependent on a number of factors that all contribute to overall fitness of the organism. Fitness is reduced to 0 when the animal is killed for example, by a predator. (Rosenberg and Bouchard, 2021).

Fix rates = time between successive locations.

FID = Flight Initiation Distance: the distance at which a prey animal, takes flight/moves away from an approaching threat (Hediger, 1964).

GIS = Geographical Information System

GPS = Global Positioning System

GPS fix(es) = the locational data provided by the GPS for a specific point. These can be 2D or 3D.

NAM = The North American Model of Wildlife Conservation

NRI = Noble Research Institute

OR = Oswalt Ranch

PTD = Public Trust Doctrine

Step length = the total distance travelled between two consecutive GPS fixes.

SWA = State Wildlife Agency

WTD = white-tailed deer

1 Introduction

Movement ecology is a growing field that helps us explore the spatial and temporal relationships between wildlife and landscapes (Nathan *et al.*, 2008). This field has important implications for building successful management plans for species, due to the relationship between movement and individual fitness of organisms. In my research I aim to answer questions about direct interactions between hunters and white-tailed deer and subsequently how these interactions alter deer behaviour in terms of both their movement response and habitat/resource selection.

The response of species to spatiotemporal predation risk caused by hunters has seen limited study but can provide important insights into human-wildlife interactions (Lima and Bednekoff 1999; Cleveland *et al.*, 2012). In the last two decades GPS (Global Positioning System) and GIS (Geographic Information System) advances have been harnessed to study many aspects of wildlife behaviour and movement (Hebblewhite and Merrill, 2007). As this technology has improved, so has our ability to study wildlife remotely at finer spatial and temporal scales allowing for new methods to be utilized in the study of movement ecology. For example, resource selection studies, which focus on identifying which resources, such as food items or habitats are used by animals in relation to the availability of those resources (Allredge and Griswold, 2006), have been carried out in multiple species (Hebblewhite and Merrill, 2007; Little *et al.*, 2014), as have predator prey relationships, however, these studies are often separate and only incorporate either spatial or temporal processes but rarely both. There are very few studies which combine predation risk and resource selection, yet such studies can be incredibly important as many taxa experience lower survival or fitness resulting from increased movement (Biro *et al.*, 2003; Taylor and Knight 2003); which, in many species, results from the landscape of fear they experience in response to predation (Laundre *et al.*, 2001, 2014; Clinchy *et al.*, 2013; Ripple and Beschta, 2003). Even with the increasing power of analysis tools, our understanding of the link between anti-predator behaviour and temporal risk at varying spatial or temporal scales is still not well defined (Picardi *et al.*, 2018).

Comprehensive assessment of these behaviours is still lacking across all species of cervid, however, of the studies which do explore these behaviours, many have focused on females and juveniles (Karns *et al.*, 2012). This has given an incomplete picture of cervid behaviour as, biologically, males and females have different life histories and energetic expenditures (Hewitt, 2015). This lack of information is a limitation for wildlife managers trying to make decisions on population management (Campbell *et al.*, 2005). Current knowledge on the efficiency of hunting and how it is affected by landscape features is limited, understanding the behaviour of deer in relation to landscape features may have important implications for hunting success, and in turn, meeting management goals.

Existing studies (Lebel *et al.*, 2012) provide conflicting advice for improving hunter efficiency whilst simultaneously decreasing deer populations. Without the presence of large predators to regulate prey populations, humans can replace mammalian carnivores as the apex predator (Schuttler *et al.*, 2016; Flueck, 2000), but to what extent? Animals should respond to anthropogenic disturbance, such as noise, objects approaching at speed and olfactory cues, in their 2002 paper Frid and Dill define the term disturbance stimulus to denote “for a human-related presence or object [e.g., birdwatcher, motorized vehicle] or sound [e.g., seismic blast] that creates a disturbance”, as they would to mammalian carnivores according to the risk disturbance hypothesis (Frid and Dill, 2002). New technologies allow us to study the influence of human predation and its effects on prey populations. By combining high resolution GPS and GIS data, the spatial aspects of cervid responses to anthropogenic hunting can be studied and new knowledge used to inform management decisions with greater accuracy than ever before (Rutter, 2007; Urbano *et al.*, 2010).

Sustainable use of wildlife populations is of importance in North America and across the globe (Decker *et al.*, 2017) and provide resources to people as a food source (Arnette and Southwick, 2015). This is true of white-tailed deer (*Odocoileus virginianus*) which thrive in mixed landscapes with both food and cover from predators. Thus, the availability of these resources strongly influences population demography (Riley *et al.*, 2003; Vercauteren and Hygnstrom, 2004). Females with access to high quality forage breed earlier and produce more offspring (Hewitt, 2015). In the absence of suitable numbers of

mammalian carnivores, lethal removal of deer is the best way to manage deer populations (Hubbard and Nielsen, 2011) and public hunting plays a large role in management strategies. White-tailed deer populations across North America have increased, to record numbers, in the last one hundred years (Cleveland *et al*, 2012; Hewitt, 2015). Increases in cervid numbers (Lebel *et al*, 2004) have led to increased human wildlife conflicts and damages from white tailed deer in areas where they exist above carrying capacity (Vercauteren, 2011). High densities of large herbivores directly affect plant communities and indirectly effect other species via trophic cascades (Ripple and Beschta, 2003).

Movement ecology allows us to combine these multiple variables, both spatial and temporal, to gain a clearer understanding of how different factors interact to influence the decisions of these species. The combination of GPS, GIS and vegetation mapping can enhance our understanding not only of how animals move but the influence of landscape and habitat features on these movements. It is known that the spatial distribution of vegetation impacts herbivore foraging and herbivores impact abundance and distribution of the vegetation (Tallowin *et al*, 2005). The risk allocation hypothesis predicts that movements will decrease in spatial and temporal scenarios with high forage and increase during times with high predation risk (Ferrari *et al*, 2009). Previous studies of movement ecology have found differing results, some found home ranges of white-tailed deer decrease during hunting season (Marantz *et al*, 2016), whilst others have found that individuals increase movement, but not home range (Little *et al*, 2014). Some species display movement responses to short term fluctuations in predation (Proffitt *et al*, 2009) whereas others present a seasonal response to risk (Ciuti *et al*, 2012). This is likely due to differences across species and different methodologies being used to study their movement (Johnson *et al*, 2004; Millsbaugh *et al*, 2000; Benhaiem *et al*, 2008) making it difficult to draw conclusions about response to predation.

Traditionally, two methodologies have been used: distance travelled using metrics such as velocity (Ciuti *et al*, 2012) or area covered using home ranges and other spatial metrics (Apollonio *et al*, 2010). Whilst both approaches are valuable and provide insight into movement in response to risk, they do not provide a complete picture of individual decision making in response to predation or disturbance. Space and time are inextricably

linked and to gain a better understanding of these factors there is a need to find ways to incorporate spatial and temporal data simultaneously, which has not been done before. Some previous studies have attempted this, using visual data, but this does not give an accurate representation of overall flight distance and resource selection (Bonnot *et al*, 2017; Preisler *et al* 2006; Taylor and Knight, 2003). In addition, greater flexibility in statistical approaches is necessary (Hebblewhite and Merrill, 2008). Some existing methodologies such as probabilistic flight response incorporate baseline patterns into movement models (Preisler *et al*, 2006) but methodologies are still being developed that will give us a more complete picture of how movement relates to spatial, temporal, behavioural factors.

Greater use of fine-scale movement metrics is now possible with improved technological and statistical power, and such research has the potential to yield novel insights on the relationship between hunting and the resulting movement behaviour and space use of large herbivores (Picardi *et al*, 2018). To draw more insightful conclusions, incorporation of control areas with no hunting when looking at movement in response to hunting is needed (Karns *et al*, 2012). This incorporation would allow more concrete conclusions to be drawn as to the effect of hunting on space use of herbivores.

My research seeks to address how human hunting – specifically proximate encounters with human hunters – alter white-tailed deer behaviour (in the short term). Specifically, I will address the following research questions looking at the movement behaviour of male white-tailed deer (i.e., bucks) in response to proximate encounters with human hunters to give a more accurate and complete picture of interactions between people and wildlife and how this may influence habitat use and fitness of bucks during hunting season:

- 1) **Do encounters with human hunters alter the movement behavior of white-tailed deer bucks (e.g., flight response)?**
- 2) **Do habitat/landscape attributes mediate the movement behavior (e.g., flight response) of white-tailed deer bucks following encounters with hunters?**

3) Does the age of bucks influence the probability of encounters occurring and/or response to encounters with hunters?

It is hypothesized that individuals are more likely to flee when the threat of human predation is close than when it is distant (Stankowich, 2008). Thus, I would also expect that flight initiation distance is related to other levels of risk such as habitat type, hunting method and hunting pressure which may in turn be linked. In addition, it is hypothesized that older individuals may display different movement responses due to learned behaviour, as it is well documented that deer can learn and remember (Jakopak *et al.*, 2019; Lewis *et al.*, 2021; Merkel *et al.*, 2019; Ranc *et al.*, 2021; Wolf *et al.*, 2009; Gillingham and Bunnell, 1989). Therefore, the expectation is that the riskier a situation is perceived to be, the greater initiation distance and flight movement, overall will be.

Quantifying disturbance of white-tailed deer by hunters will enable a better understanding of these interactions and the subsequent changes in habitat use and trade-offs between anti-predator behaviour. Studying the response to interactions at this level allows us to analyse individual movements without losing the nuanced differences in movement patterns. Overall, this will allow a greater understanding of behaviour and provide information to improve the accuracy of management plans for wildlife populations, as well as to understand how behaviour influences physiology and fitness of individual WTD.

Gaining a better understanding of spatial movement behaviour of wildlife is paramount to improving wildlife management, not only for hunters but for a diverse set of stakeholders. Cervids especially have a large role in biogeochemical cycling (Popma and Nadelhoffer 2020; Harrison and Bardgett, 2008) and managing their numbers adequately, through hunting, ensures that these ecosystem services would be retained whilst also considering the balance needed to minimize damages caused by sustained populations above carrying capacity. Inclusion of anthropogenic impacts and influences is also necessary to gain a full understanding of interactions between cervids, humans and landscapes.

It is not just the presence of consumptive users who impact the spatial ecology of wildlife. Wisdom *et al* (2018) shows that trail-based recreation led to spatial avoidance of those

areas by Elk (*Cervus elaphus*). The methods used to understand of spatial interactions between consumptive users and deer, could be transferable to non-consumptive users. Such data will be incredibly useful in the future of natural resource management as the urban/rural interface becomes increasingly blurred.

2 Background

As new technology and understanding of complex biological systems is developed, so too should management of wildlife populations be amended and advanced. Developments in GPS and GIS technologies allow the study and modelling of more complex processes which could improve management of not only WTD but also many other wildlife species. Managing and conserving important ungulate game species into the future depends on an accurate understanding of the complex spatial interactions of WTD with hunters and other recreationalists.

2.1 History of the North American Model of Wildlife Conservation (NAM)

The North American Model of Wildlife Conservation (NAM) (Organ *et al.*, 2012), has been extremely successful at increasing numbers of certain game species, through a tag allocation system for hunters. So successful, in fact, that White Tailed Deer are thriving to the point of overabundance in many parts of their range (McShea and Rappole., 1997; Vercauteren, 2011). The original premise was to promote the sustainable use of wildlife as a resource through its regulation and management, for the future of all North Americans.

The NAM is a unique model implemented throughout the US and Canada (Organ *et al.*, 2012)

This model is based on 7 principles:

- 1) Wildlife is a public trust resource
- 2) Markets for game shall be eliminated
- 3) Allocation of wildlife is by law
- 4) Wildlife can only be killed for a legitimate purpose
- 5) Wildlife is an international resource
- 6) Science is the proper tool to discharge wildlife policy

- 7) Democracy of hunting is standard (Reduction in and access to huntable lands comprise the principle of egalitarianism in hunting opportunity – Restrictive firearms legislation can act as a barrier to participation) (Organ *et al.*, 2012)

In the United States, the federal government has a primary responsibility for migratory birds, marine mammals and species that are listed as federally endangered under the Endangered Species Act (Decker *et al.*, 2015). Wildlife management of other groups subsequently falls to individual states (Decker *et al.*, 2015). Within Canada, provinces oversee wildlife management to differing extents (Organ *et al.*, 2012). With this responsibility comes the assumption that managers will make decisions that are objective, informed (Decker *et al.*, 2015) and in keeping with the principles of the NAM.

Whilst this concentration on hunting and fishing has historical precedent and has led to the success of game species' populations rebounding to what is seen in North America today, it has drawn criticism in recent years, and not without good reason. The interpretation of the NAM has continued to be overly narrow since its inception (Serfass *et al.*, 2018). The overreliance on consumptive users for funding, through the Pittman-Robertson excise tax (Serfass *et al.*, 2018), and consultation of wildlife management decisions due to the model, is problematic. The widely asserted idea that hunters and anglers saved America's wildlife is an example of this selective overemphasis on the contributions of consumptive users (Hewitt, 2015). Though this funding model has been largely successful in meeting the aims of what it set out to do, fund the conservation of game species (Hewitt, 2015).

This narrow focus of the NAM on game species only is what led to the Conservation Biology movement of the 1960's – 1990's, which was largely led by non-traditional stakeholders (Peterson and Nelson, 2016), seeking to protect the species which were not a focus of the NAM. Many conservation organisations contributed to the prosperity of wildlife in North America, from pushing for the creation of federal acts such as: the Clean Air Act, the Clean Water Act and the Endangered Species Act which have all contributed to the protection of wildlife and lands, and the creation of The Fish and Wildlife Conservation Act of 1980 which was termed the "Non-game Act" (Serfass *et al.*, 2018), to the creation of organisations such as the Society for Conservation Biology (SCB) in

1985. In fact, the contribution of federal legislature for land management, and in turn wildlife, is often understated (Serfass *et al.*, 2018).

Although there is the suggestion that states manage wildlife and federal land agencies only manage wildlife habitat (Nie, 2004) this has several problems in practical implementation. Wildlife do not recognise our anthropogenic parcelling of land into 'Federal', 'State' and 'Private' and as mobile agents they can move between these different designations with relative ease, unless barriers such as fences prevent their movement. Additionally, it was the federal government who enacted the Endangered Species Act (ESA) (1973), which is widely accepted as a powerful instrument for species conservation (Treves *et al.*, 2017). The ESA is not part of the NAM and prioritizes the preservation of species over economic considerations which can lead to push back from some interest groups (Treves *et al.*, 2017). The development of the ESA additionally pushed states to create and enact their own regulatory statutes regarding species conservation (Treves *et al.*, 2017). Furthermore, most public land agencies (National Forest Service, US Fish and Wildlife Service, Bureau of Land Management and National Park Service) which preserve these wildlife habitats are not, in fact, funded through the Pittman-Robertson or other hunter derived monies, they are funded through general tax revenues (Serfass *et al.*, 2018). Therefore, there seems to be a significant amount of disjunction between State Wildlife Agencies (SWAs), funded largely by consumptive users, with the mandate of wildlife management (in theory, in keeping with the PTD) and federal management agencies who are funded by general taxes with the mandate of managing lands for wildlife within the PTD.

One of the seven principles is that information for wildlife management still predominantly comes from scientific research (Lute and Gore, 2014). How that is applied, however, and by who is not always so simple. Lute and Gore (2014) shows there is disagreement over whether resident and hunter interests were considered too much or too little in wildlife management decisions. Where there is disappointment in the results of natural resource management decisions, it can lead to public mistrust of SWAs (Miller and Nadeau, 2017). This, in addition to path dependencies due to historical mandates between hunters and SWAs can lead to distrust of the real loyalties of wildlife

management professionals and whose interests they truly serve (Jacobson, 2008). This it is important that scientific information and studies are open and available to the public. On the other hand, some in SWAs are concerned that sustainable use will cease to persist, in part due to the declining number of traditional stakeholders who contribute to the model (Decker *et al.*, 2017).

Management that has failed to manage to a diverse stakeholder community has led, in part, to White Tailed Deer exceeding both their biological and social carrying capacity in many areas (Vercauteren, 2011) as has habitat augmentation and agricultural development, this chasm in stakeholder interests can be exemplified by crop damage, it is not just a rural urban dichotomy at play. Damage to crops by White Tailed Deer in 13 states within the North-eastern US was found to be \$172 million per year, in that geographic area alone (Hygnstrom *et al.*, 2013) whilst wildlife vehicle collisions involving deer cost \$3.1 billion annually in the US (Gilbert *et al.*, 2016).

2.2 Hunting as a management tool

A cornerstone of the NAM is the use of hunting as a management tool. Hunting can assist managers in reducing populations of deer in these areas (Lebel *et al.*, 2012) and is a socially acceptable practice with high economic returns (Brown *et al.*, 2000). The effects of anthropogenic hunting tactics in comparison to those of mammalian predators have important consequences for wildlife management and conservation (Cromsigt *et al.*, 2013). Given the complex spatial interactions between ungulates, vegetation, abiotic factors, and management (Kramer *et al.*, 2006), there is still a need to gain a more detailed understanding of how hunting impacts both deer populations and achievement of management goals, to ensure longevity sustainable use.

The use of hunting as a management tool has both direct and indirect effects on animal behaviour, life history and demography (Creel and Christianson, 2008; Darimont *et al.*, 2009). Unlike mammalian carnivores such as wolves, predation by humans is temporally confined to hunting season (Cleveland *et al.*, 2012), which may also limit the extent to which hunting can meaningfully impact the population. In addition, responses to hunting pressure may only be apparent after a certain threshold of hunters is reached (Root *et al.*,

1988), so previous studies have included a range of hunting pressures (expressed as a function of hunters/km²) (Diefenbach *et al.*, 2005; Little *et al.*, 2016) there is yet to be conclusive evidence of what this threshold may be. The vulnerability of individuals to harvest is the combination of several biotic and abiotic factors including, but not limited to, the movement of deer, habitat cover, sex, hunter density, topography, and forage availability (Karns *et al.*, 2012; Lebel *et al.*, 2012). Whilst previous studies have addressed these factors individually, literature does not include studies of these factors in a combined manner.

For rangelands in particular, outcomes can be most effectively determined by selective and systematic monitoring of both production and environmental quality linked to the detection of landscape level consequences (Briske *et al.*, 2017). As wildlife management professionals, we must not only seek to be critical of ourselves but use best practices for both research and consulting. Agencies must also seek to improve how they communicate with wider stakeholder groups (Campbell and Mackay, 2009). This must be done in a way that is accessible to stakeholders which may not have a good grasp on wildlife dynamics as traditional stakeholders might.

The effort to include wider interests must not be done at the expense of alienating traditional stakeholders. Lethal removal of deer is the best way to manage deer populations (Hubbard and Nielsen, 2011) and this tool should continue to be utilised this into the future. Although, the efforts of SWAs in Wisconsin have been with limited success. Hunters are reluctant to exceed their own take threshold (the number of deer they can process/adequately use) (Holsman and Petchenik, 2006; Van Deelen *et al.*, 2010) and hunters may withdraw their participation of management efforts if they perceive the goals for lower densities to be counter to their own interests (Vercauteren, 2011). In previous studies which have focused on hunter perspectives, several factors have been identified which contribute to hunter experience and success of harvest: abundance of forage for deer, visibility of the deer from the hunter vantage point and accessibility of the land (Lebel *et al.*, 2012). Understanding exactly how hunters affect deer populations however, not just through mortality but through other effects such as displacement and, potentially,

decreases in fitness due to increased energy expenditure will enable managers to create more accurate targets to meet their goals.

2.3 Deer ecology and behaviour

Harvest objectives from SWAs have historically been based solely on models of ungulate populations without consideration for ecosystem effects of herbivory (Weisberg *et al.*, 2002) yet white-tailed Deer have severe impacts on: garden plants, native vegetation, non-timber forests and plant nurseries compaction of soil, wildlife vehicle collisions or the transmission of zoonoses (Bernes *et al.*, 2018; Tanentzap and Coomes, 2011; Vercauteren, 2011). Even if just considering herbivory, the relationship between food webs and spatial movement of ungulates is crucial to understanding meta ecologies (Massol *et al.*, 2011) which allow us to gain insight into natural resources at a landscape scale.

Managing to increase hunter success by creating openings in the forest would make hunting more efficient (Lebel *et al.*, 2012) which, in theory, would be beneficial in trying to reduce deer numbers. Yet caution should be exercised in the of opening up previously forested habitat, as this may be counterintuitive when deer biology is considered. Habitat augmentation may lead to increased forage availability for deer, compensatory mechanisms therefore may offset any additional mortality incurred through improved hunter efficiency (Boyce and McDonald, 1999) which in turn could improve fecundity. Does with access to high quality forage breed earlier than counterparts with access to lower quality forage, deer have high biotic potential and can breed as early as 6 months of age when feeding on high quality forage vs 18 months of age without, in fact, in the presence of optimal conditions deer may see an annual increase of 89% in populations (Hewitt, 2015). White-tailed deer are influenced by amount of forest cover and availability of agricultural food resources (Vercauteren and Hygnstrom, 2004). They thrive in mixed landscapes where both food and cover from predators are readily available to them (Riley *et al.*, 2003) having food without cover or vice versa would impede their success. Thus, armed with this understanding it becomes clear that making changes to habitat that may benefit hunters, could have unforeseen consequences and in fact, grow the deer population. Such queries exemplify the need to gain a complete

understanding of spatial interplay between deer, hunters, recreationists, and habitat augmentation by wildlife managers. Whether one is trying to increase or decrease the population of deer or keep them from certain habitats such as crops or lumber nurseries, understanding how deer move and what motivates such movement is critical.

Studies have also shown that sex plays an important role in deer biology, Anderson (2010) observed slight differences in habitats used by male vs female deer and found that females used certain habitats, such as wetlands, more so than males. Studies have also found that deer vulnerability to harvest displays an inverse relationship with forest cover % (Foster *et al.*, 1997). Therefore, sex specific differences in habitat selection may be related to harvest vulnerability and movement in response to interaction with hunters and should be considered, especially as deer tags are often given based on sex.

Deer in some cases can be a causal factor in the prevention of forest regeneration, decreases in songbird numbers (due to lack of habitat), lowered aesthetic attributes of ecosystems and increased damage to crops (Riley *et al.*, 2003). Some of these issues can be demonstrated via the reintroduction of wolves in Yellowstone. Since predators were removed from much of their historic range in the US due to their competition with hunter and livestock owner interests. In Yellowstone the landscape became degraded due to overgrazing by ungulates (Ripple and Beschta, 2004), this damaged the aesthetic value of the park as well as ecosystem processes within it. When wolves were reintroduced, there was a cascading effect that created greater movement of ungulates, less overgrazing of vegetation and subsequently increases in bird number and beaver activity (Ripple and Beschta, 2004) highlighting the importance of movement to larger biological impacts of these species.

Management of parks and refuges is also important regarding how ungulates move between and within them. Wildlife refuges were found, in some cases, to have deer populations as great as four times the surrounding areas (Riley *et al.*, 2003). This could be for several reasons to do with access and management and behavioural changes in the deer such as human shield effect which has been observed in ungulates (Berger, 2007). Deer have shown spatial avoidance to hunters (Sullivan *et al.*, 2018) so, if refuges have no hunting and the surrounding areas do, you may end up with a concentration of

ungulates due to decreased predation risk (Lone *et al.*, 2015). This can have important implications not just for herbivory impacts but also for the spread of zoonoses, CWD is becoming increasingly prevalent across North America and is of great management concern, not only will the disease agent be passed between individuals more readily where they are allowed to congregate in such densities, the disease agent can be highly persistent in the environment also (Belay *et al.*, 2004). Additionally, ungulates especially have a large role in biogeochemical cycling, these relationships with nutrient cycling are non-linear (Pastor and Bridgham, 1998), and managing their numbers adequately ensures that these ecosystem services would be retained whilst also considering the balance needed to minimize damages caused by excessive numbers.

Movement decisions can have a direct effect on fitness. Where to move and when have costs and benefits which may not be fully understood at present. Individuals that use too much caution in response to predation can risk nutritional deficiency as increased vigilance decreases grazing time. Conversely, individuals who use too little caution (and subsequently spend more time grazing) risk injury and death (Sullivan *et al.*, 2018). High levels of predation risk can influence survival and reproduction by causing the diversion of time and energy away from resource acquisition. It is not just the direct cost of predation which may influence movements, the risk of predation itself may affect population dynamics by indirectly altering anti-predator behaviours (Gill and Sutherland, 2000).

Whilst the Landscape of Fear (LOF) was described by Ripple and Beschta (2004) pertaining to the movement of prey in response to mammalian predators, more recent studies have also documented this effect in response to anthropogenic harvest. Sullivan *et al.* (2018) found both spatial and temporal responses could be found to be predictable when human hunting pressure was evident. However, responses were only evident when also considering the localised nature of the risk. There is still some argument as to how movement responses increase or decrease risk to the individual. On the one hand, it has been argued (Roseberry and Klimstra, 1974) that increased movement actually increases the likelihood of deer encountering a hunter and thus suffering predation. Conversely, it

has been argued that increased movement allows animals to move between resource patches and avoid predation (Sullivan *et al.*, 2018).

Frequent anthropogenic disturbance has consequences for energy expenditure and survival of individuals, especially in winter when resources are scarce in temperate climates, energy available for lactation for young and the rebuilding of mass after the winter (Cook *et al.*, 2004) leading to impacts on population demography. Combined with high hunter densities and long hunting seasons, these effects can be exacerbated (Johnson *et al.*, 2004). Depending on management goals these decreases in fitness may be beneficial or detrimental to overall population augmentation goals. Subsequently, understanding how resource selection functions can interact with energy expenditure is important to future management.

2.4 Ecology of fear (anti-predator responses in wildlife)

The scale at which a deer exhibits a response is a function of the level of risk in the system and anti-predator responses subsequently exist in a hierarchy (Picardi *et al.*, 2018). In addition to predation, movement can also be influenced by other factors such as seasonal food availability and reproductive stage (Frair *et al.*, 2005; Lebel *et al.*, 2012). Individuals must make trade-offs between habitats which offer cover from predators and forage availability with the seeking of mates and avoiding human disturbance (Gill *et al.*, 2000). Resource selection functions may also vary by geographic location (Hebblewhite and Merrill, 2008) therefore, conducting studies at appropriate spatial scales is important for identifying the processes occurring.

As Ripple and Beschta (2004) have showed in their seminal work, prey behave differently to mammalian, non-human predators such as wolves, by increasing spatial and temporal movement and subsequently redistributing browsing pressure. This area of research continues to grow as we learn about non-lethal predation effects in wildlife populations (Clichy and Zanette., 2019; Clinchy *et al.*, 2012; Horta 2010; Gaynor *et al.*, 2021; Daversa *et al.*, 2021). Whilst the original works on the Landscape of Fear (LOF) described by Ripple and Beschta (2004) pertained to the movement of prey in response to mammalian predators, more recent studies have also documented this effect in response

to anthropogenic harvest. Sullivan *et al* (2018) found both spatial and temporal responses could be found to be predictable when human hunting pressure was evident. However, responses were only evident when also considering the localised nature of the risk. There is still some argument as to how movement responses increase or decrease risk to the individual. On the one hand, it has been argued (Roseberry and Klimstra, 1974) that increased movement actually increases the likelihood of deer encountering a hunter and thus suffering predation. Conversely, it has been argued that increased movement allows animals to move between resource patches and avoid predation (Sullivan *et al.*, 2018).

As the human population grows, people increasingly come into contact with wildlife. Such encroachment by humans on natural habitat can have a number of impacts on wild populations - for example, through habitat alteration and through the animal's stress response to fear of being preyed by humans. This 'landscape of fear' (Ripple and Beschta, 2004) can negatively affect the fitness of animals by imposing new costs on their naturally evolved life histories (Creel and Christianson, 2008). Animals must continuously balance time spent foraging or caring for offspring with self-preservation and defence. The optimal balance is shaped by selection, but human encroachment can upset this balance and force animals to invest more heavily in defence at the expense of growth and reproduction (Verdolin, 2006; Hebblewhite and Merrill, 2009). These costs potentially reduce lifetime fitness of individuals and populations, leading to their decline. Accordingly, optimal escape theory predicts that animals under threat of predation will initiate their escape response at a distance that minimize disruption yet maximize success (Ydenberg and Dill, 1986). If so, prey are expected to adjust their escape response to optimize this trade-off such that the strongest threats provoke the earliest response (Cooper and Frederick, 2010; Hemmi and Pfeil, 2010). At present, however, the impacts of anthropogenic disturbance on behaviour, population dynamics and life history remain poorly documented (Ciuti *et al.*, 2012).

Deer and other ungulates provide a good model to study the landscape of fear on variation in escape response. The deer family Cervidae, in particular, is vulnerable to human encroachment because their free-roaming populations are a target for hunting and wildlife tourism. Many previous studies have been qualitative or have used methodologies that

give an incomplete picture of how this taxonomic group respond to anthropogenic predation risk. A meta-analysis by Stankowich (2008) found most studies have only been carried out on one a single species with no replication in other species in the taxon using the same methodology. The lack of consistency in methodology and breadth of study species make it difficult to draw meaningful conclusions about the cost of antipredator behaviour to large herbivores as a group. Elk (*Cervus elaphus*) have been found to be sensitive to human disturbance, whilst White-tailed deer are regularly found in association with human habitation (Ciuti *et al.*, 2012; Walter *et al.*, 2011).

Additionally, it has been found that herbivores in open habitats have a greater flight initiation distance - “flight initiation distance (FID, the distance between the observer and the animal when it decides to flee” – (Jammes and Blumstein 2012) than those in closed habitats (Stankowich and Coss, 2006); and that females with young will flee more readily than males (Frid and Dill, 2002). Stankowich (2008) additionally reported that ungulate flight distances are dependent on multiple factors including speed of hunter approach and individuals’ perception of risk, which may differ amongst populations dependent on their previous exposure to anthropogenic disturbance. Stankowich (2008) found that ungulates in hunted populations displayed greater flight distance than non-hunted populations.

2.5 Spatial ecology

A study on the spatial ecology of White-tailed deer by Marantz *et al* (2016) shows deer, at least in hunting season, decrease their movement. Other studies (Stankowich, 2008) show ungulates in hunted populations have a greater flight response than non-hunted populations and research by Little *et al* (2014) showed White Tailed Deer can avoid hunters by changing resource selection patterns. The distinction between anthropogenic and non-anthropogenic predation, is an important one. Whilst mammalian predators such as wolves promote greater movement of prey species, human predators might, in fact, have the opposite effect. As Marantz *et al* (2016) found, WTD during hunting season decrease the size of their home range and subsequently their movement.

Studies such as Keenan *et al* (2008) have found spatial relationships, not only between hunters and deer but between landscape features and land management agents. On public

lands it was found that harvest rates, and presumably interactions, for deer declined farther from roads and on steeper slopes. However, on private lands roads had minimal relationship to harvest rate yet deer on steeper slopes continued to encounter lower harvest rates.

Other studies such have shown mixed results concerning anthropogenic impacts on ungulate spatial ecology. Bleisch (2014) used hunter and Elk GPS data to consider the spatiotemporal interactions between the two. In this specific study it was found that Elk responded to the presence of hunters by utilizing refugia. Thus, there are multiple ways in which ungulates may react to hunter presence and seek out refugia whether that be different habitat (forest) or different elevation. This concept of refugia in ungulate spatial ecology is echoed by Keenan *et al* (2008) who found that spatially variable rates of harvest can also create a type of refugia for individuals that allows them to avoid hunter induced mortality. Whilst refugia, and the factors which may create them, are an important consideration, it is also necessary to consider the technological issues which may influence data deficiency and therefore, create the appearance of effects that do not truly exist. Battery failure, faulty release mechanisms, failure of components within the electronics and poor signal strength may provide a false impression of what is truly occurring on the ground.

There remains a limited understanding of how prey respond to human hunters on the landscape. With increasing technological ability allowing the collection and interpretation of more complex and fine scale data, this can contribute to greater understanding of the interactions between people and wildlife. Whilst Marantz *et al* (2016) shows a decrease in movement during hunting season this study did not incorporate habitat types. Given the complex spatial interactions between ungulates, vegetation and abiotic factors and management (Kramer *et al*, 2006), gaining a better understanding of spatial movement is paramount to improving wildlife management for a diverse set of stakeholders.

As Organ *et al* (2012) suggests, going forward, conserving not only wildlife but including landscapes in the future of the NAM will be key to its success. Inclusion of anthropogenic impacts and influences is also necessary to gain a full understanding of interactions against landscapes.

It is not just the presence of consumptive users who impact the spatial ecology of wildlife. Wisdom *et al* (2018) shows that trail-based recreation led to spatial avoidance of those areas by Elk (*Cervus elaphus*). The understanding of spatial interactions between non consumptive users and wildlife is growing. Yet understanding of intensity of effects at most spatial and temporal scales that could be meaningful to wildlife is still limited (Gutzwiller *et al.*, 2017).

3 Methods

3.1 Study Area

Data was collected at the 1,861 ha Oswalt Ranch (OR) owned by Noble Research Institute (NRI), in Love County, Oklahoma (Fig.1). The property is located in the Cross Timbers and Prairies eco-region which is defined by a mixture of woodland (e.g. oaks [*Quercus spp.*], elms [*Ulmus spp.*], and hickories [*Carya spp.*]), valley bottoms (e.g. various oaks, ashes [*Fraxinus spp.*], elms, and hackberries [*Celtis spp.*]), uplands (gramas [*Bouteloua spp.*], bluestems, dropseeds [*Sporobolus spp.*] and Texas Wintergrass [*Nassella leucotricha*]) and open rangelands (e.g. mixture of bluestems [*Andropogon spp.*], switchgrass [*Panicum virgatum*], Indiangrass [*Sorghastrum nutans*], and numerous forb species (Little *et al.*, 2016; Gee *et al.*, 2011). The OR itself is composed of a rural landscape with minimal linear features such as gravel, dirt, and paved roads (density = 1.4 km/km²) with elevations between 233m and 300m and slope from 0° to 41°. At the time of data collection, the ranch was non-operational without grazing by cattle or prescribed fire management. Other sources of potential predation include coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) occurred in the study area.

3.1.1 Cross Timbers eco region

The Cross Timbers eco region, which the study area falls within, stretches 700 miles from southern Kansas to Texas and makes up more than half of the forest types in Oklahoma (Hoagland, 2000). The characteristic mix of forest, woodland and grassland is ideal habitat for white-tailed deer who are known to be edge species (Williamson and Hirth, 1985). This edge habitat and mix of open areas and closed canopy allows deer to meet the spatial and temporal needs of their life histories. Within the overstory, trees are small in

stature with the top of the canopy reaching between 12 and 14 m. Closed stands, in this area, can attain a basal area of 23 to 27 m²/ha and average diameter at breast height of 14 to 17cm, and tree density ranges from 1400 to 1800 trees/ha (Hallgren *et al* 2011). This provides ample cover for deer trying to avoid detection or escape predators.

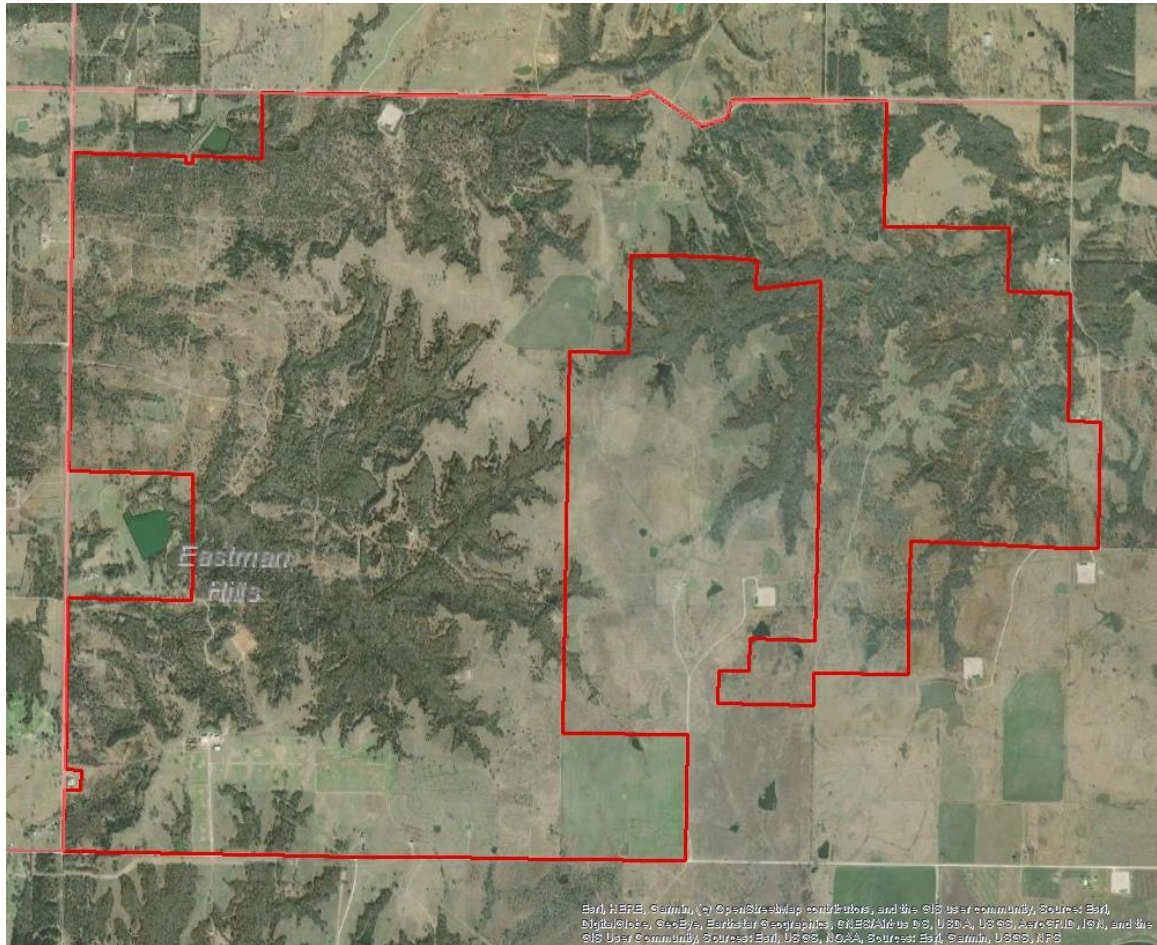


Figure 1 Boundary of the study area formed by the perimeter of the Noble Research Institute Oswalt Ranch, located in Love County, Oklahoma with a total area of 1,861 ha.



Figure 2 The boundary of Love County (33.9858° N, 97.2221° W), shown in red, located in South-eastern Oklahoma bordering Texas. This area is within the Cross Timbers ecoregion, which stretches from Kansas to Texas.

3.2 Hunting Pressure Treatments

Data used in this study was collected by Dr Andrew Little and Dr Stephen Webb for research that looked at hunting pressure and deer movement responses. As such, when the data were collected there were experimental treatments within the study area which were not the primary focus of this research. Between 2006 and 2008 when this data was collected, lease hunting was restricted to prevent carry over of effects from previous hunting risk (Little *et al.*, 2014). The Oswalt Ranch (OR) was divided into 3 risk categories based on hunter pressure: no risk (control; 679 ha), low-risk (1 hunter/101 ha; 585 ha), and high-risk (1 hunter/30 ha; 583ha) based on landscape features within the study area (Little, 2011).

Percentage cover of vegetation classes (forest, mixed forest/grassland, and grassland) was similar across all treatment levels. The low-and high-risk treatments were further divided into smaller hunter compartments comparable to the desired risk levels, to uniformly distribute hunter effort within each treatment. In the second year, treatments were shifted

clockwise to prevent habituation of deer to treatments. Hunting effort varied on surrounding properties each year, ranging from none to high-risk (Little, 2011). The majority of contacts were spatially distributed in high hunter pressure treatments (Fig 3, 4).

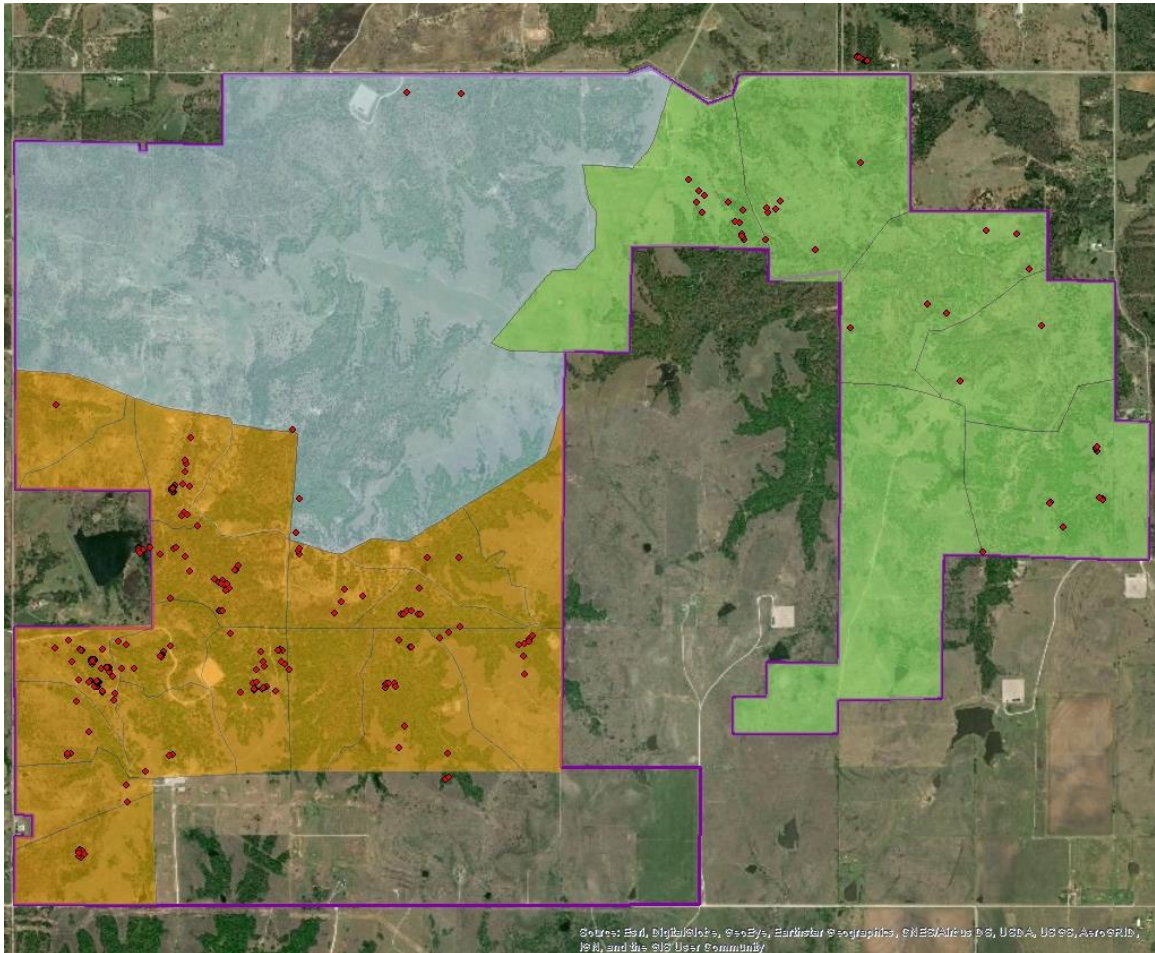


Figure 3 Samuel Roberts Noble Foundation Oswalt Ranch with hunting pressure treatments (control (blue) = no hunters on 679 ha; low-risk (green) = 1 hunter/101 ha on 585 ha; and high-risk (orange) = 1 hunter/30 ha on 583 ha) compared with point data for contacts at 150m (in red) during 2008, located in Love County, Oklahoma, USA.

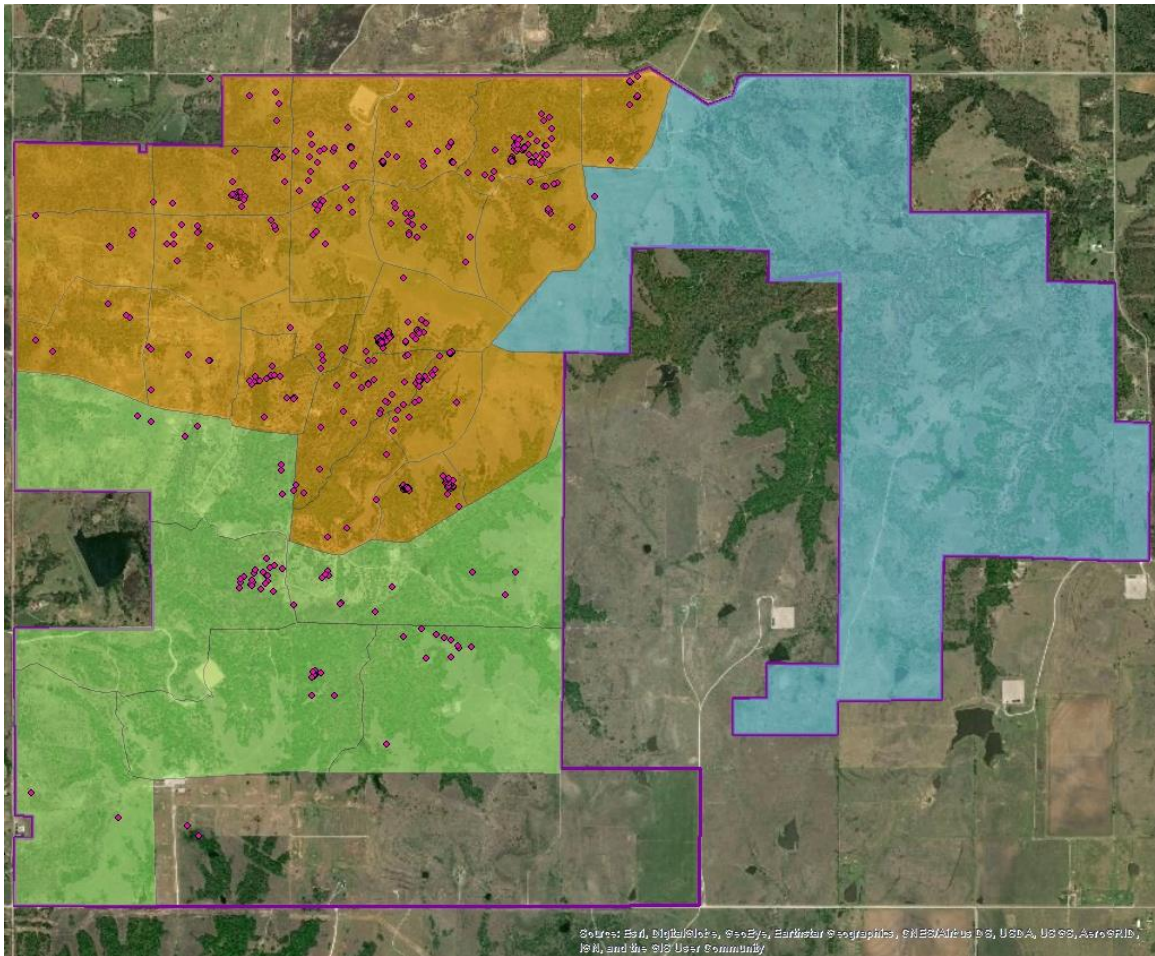


Figure 4 Samuel Roberts Noble Foundation Oswalt Ranch with hunting pressure treatments (control (blue) = no hunters on 679 ha; low-risk (green) = 1 hunter/101 ha on 585 ha; and high-risk (orange) = 1 hunter/30 ha on 583 ha) compared with point data for contacts at 150m (in pink) during 2009, located in Love County, Oklahoma, USA.

3.3 Data

Data for this study was collected by The Noble Research Institute (NRI) and collaborators from University of Lincoln, Nebraska, and Mississippi State Deer Lab. The study site is a private property owned by NRI, which allows them control over who accesses the site. Previous to the study there was no hunting allowed on the property. Data was collected in both 2008 and 2009.

3.3.1 Capture and handling of deer

Deer were captured (on the property of the OR) in the winters of 2008 and 2009 using baited drop nets and techniques for tranquilizing animals, as approved by the Institutional Animal Care and Use Committee at Mississippi State University (protocol No. 07-034). A total of 52 adult bucks were captured over the two winters of 2008 ($n = 25$) and 2009 ($n = 27$).

Deer were aged according to tooth replacement and wear (Little, 2011), but due to variations, were classified as ≥ 1.5 years at capture, and all deer were ≥ 2.5 years of age by the study period. Deer were sedated using an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Little, 2011). Prior to release, they were weighed, ear-tagged, and assigned a GPS collar.

3.3.2 GPS tracking data of deer

Following capture, deer were fitted with GPS collars (ATS G2000 Remote-Release GPS, Advanced Telemetry Systems, Isanti, MN). GPS collars were programmed to take one GPS location fix every 30 hours throughout the year, and this temporal resolution was increased to one location every 8 minutes, starting on November 7, and continued through the study season in each respective year. Each fix location provided Universal Transverse Mercator coordinates, date, time, fix status, position dilution of precision, and horizontal dilution of position. Collars were programmed with a mortality sensor that indicated inactivity after 8 hours. Any 3-dimensional fixes with position dilution of precision values > 10 and 2-dimensional fixes with position dilution of precision values > 5 were removed (Little, 2011).

Hunting season in the years the study took place was during November and December with the respective date ranges (22/11/2008 to 7/12/2008 and 21/11/2009 to 6/12/2009). In total, 270,149 GPS location fixes were collected on white tailed deer (133,790 in 2008 and 134,652 in 2009). Of these fixes $91435/270149 = 33.84\%$ (45,136 in 2008 and 46,299 in 2009) were in the hunting season. To exclude potential bias in movement distances, number of GPS fixes per hour (i.e., 1 to 8 fixes) was evaluated and hourly values with < 7 fixes/hour were removed because movement distances were biased low (A. R. Little,

personal observation; Little, 2011). The GPS tracking data during hunting season was collected with a high fix success rate, over 98% in 2008 and over 94% in 2009 of attempted fixes were successfully collected, making these data highly suitable for analysing fine-scale movement patterns.

For more detailed information on the deer data, and previous analysis of these data, please refer to (Little *et al.*, 2014; 2016; Marantz *et al.*, 2016) and additional papers are currently in progress.

3.3.3 GPS tracking data of hunters

To enable the identification of contacts, simultaneous GPS tracking data from hunters was needed. Hunters were assigned a GPS unit before the start of their hunting session, and these were returned at the end of each session to be charged. Due to the ability to keep the GPS units charged, hunter GPS fixes were able to be collected more frequently than in deer, every 1 minute.

There were 508 hunting sessions total (221 in 2008 and 293 in 2009). Twenty-two of these were classified as all day, 212 were Evening and 280 were morning. 79.96% of these took place in High hunting pressure treatment areas (411/514) and the remainder took place in low treatment area. The mean number of fixes per hunting session was 295.417 and each session lasted on average ~308 minutes. There were no hunter GPS records in the control zone. Over both years this equalled a total hunter effort as 130,176 minutes or 2,169 hours, however, this was not consistent over this entire time.

Hunter effort was calculated (i.e., hours/hectare/day) by dividing the number of hunted hours within each treatment, by treatment size, for each day. Additionally, hunter effort within each treatment was calculated by hunter exposure (i.e., initial and prolonged) to quantify effort during the hunting season. 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 (Little, 2011).

Hunters were assigned single compartments for the hunting season and were required to spend at least 4 hours per day per compartment during the weekend (Little *et al* 2014). Whilst hunter densities were maintained on weekends, on weekdays hunting pressure remained variable. Hunters were not allowed to harvest collared deer to maintain sample size, but the risk of harvest was created by allowing 20 antlerless and 3 mature, antlered bucks that were not collared to be harvested each year, except in 2009 when hunters were allowed to take 4 antlered deer.

3.3.4 Landscape Attributes

A vegetation type map was created by Little (2011), using 2009 growing-season National Agriculture Imagery Program aerial imagery, with 1-meter resolution grid re-sampled into a 17-meter resolution grid using ERDAS Imagine 9.3 (ERDAS, Inc, Atlanta, GA) software. Reclassification to 17-meter resolution was on fractal analyses (Webb *et al.* 2009) with this being the smallest patch size perceived by deer and because most location errors were ≤ 3.7 meters (Little, 2011).

The visual obstruction of each of the 3 landcover types: forest, mixed forest/grassland (Mixed), and grassland was tested using a 1.8m Nudds density board (Nudds, 1977) at 90 stratified, randomly placed vegetation plots (i.e., 30 in each cover type) 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 at a standardized height of 1.5-m and obstruction was estimated in 20% increments for each section. Classification of vegetation types corresponded to visual obstruction, which provided a range of percentage of obstruction for each vegetation type (Little, 2011)

Raster data comprising of landcover categories were created using aerial images from the US Department of Agriculture Geospatial Data Gateway and all layers had 30m pixels, this was chosen based on the spatial scale able to be perceived by deer, the half width (15m) being the smallest patch size used by deer (Little *et al.*, 2014; Webb *et al.*, 2009) and accounted for the most GPS error (Little, 2011). Landcover was classified based on the predominant use or cover type in that cell and each cell was only assigned one classification (Table 1).

In addition to these vegetation-based landscape attributes topographical variables - slope, elevation and roughness were also calculated and extracted for each GPS location of the deer using Intersect to Point within Hawth's Tools (Little *et al.*, 2014), Spatial Analyst in ArcGIS 9.3 and a 10-m resolution DEM from the U.S. Department of Agriculture-National Cartography and Geospatial Center (Little, 2011).

Roads that hunters used within and bounding the study area were delineated (i.e., dirt, stone, and paved) and using ArcGIS 9.3, all deer GPS locations were spatially joined to the nearest roadway (Little, 2011). Traffic was greatest during early morning and evening hours coinciding with hunters entering and leaving the field.

The classes of landcover were categorized as follows (Little *et al.*, 2014) (Table 1):

Table 1 Landcover categories and associated raster values based on work in Little *et al.*, 2014 and Little, 2011. The criteria and definition of each category explains how the habitat types were defined for each class.

Class	Landcover
0	Off property: Pixels outside of the study area boundary of Oswalt Ranch.
1	Mixed: trees, shrubs, and sections of open area such as grasslands/herbaceous vegetation with less than 70% of both closed canopy (forest) and open areas (grassland).
2	Forest: greater than 70% closed canopy cover
3	Field (grassland/herbaceous vegetation):
4	Non habitat: bare ground, cleared areas, gravel/sand pits.
5	Road: paved or gravel road (dirt two track was not included in this).
6	Anthropogenic: buildings, barns, homes etc.
7	Pond: standing bodies of water that are permanent (natural lakes, man-made ponds etc).
8	Riparian: streams and rivers using a 25m buffer on either side of the centre line of the feature.

Due to the timing of the study, predominant tree species (oaks) still retained foliage. In this area of the eco region, oaks do not lose their leaves until January or February (Francaviglia, 2011).

The movement tracks of bucks were overlaid with the habitat raster, provided by Dr Little and Dr Webb, to extract habitat variables associated with each GPS fix during the study period. Using this information, these were incorporated into the final analysis that was completed to better allow an understanding of the influence of vegetation types and land use on deer response to hunters.

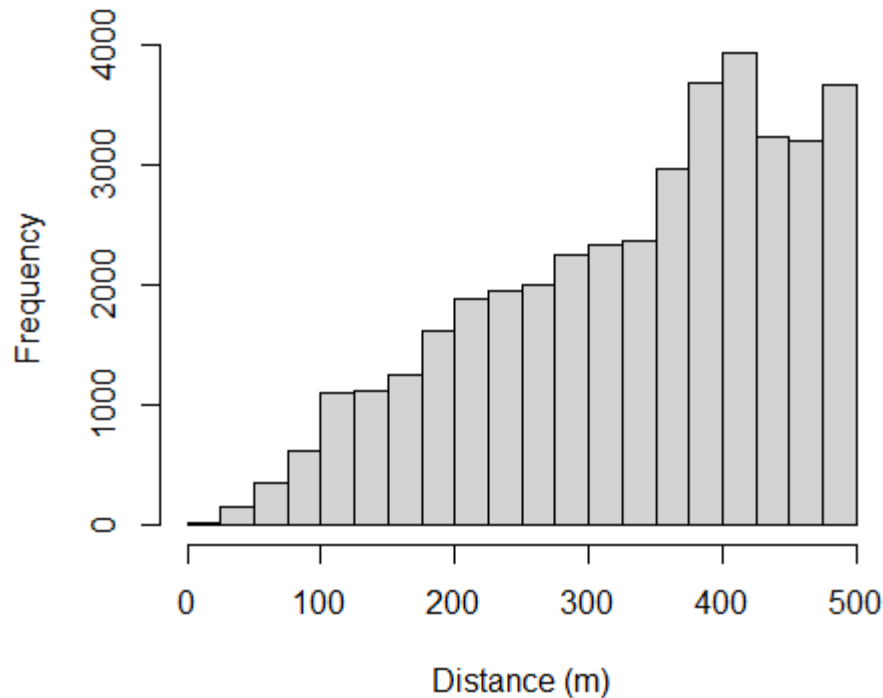
3.4 Identifying spatial temporal contacts

I used the GPS tracking data of the deer and hunters to identify spatial-temporal encounters, to study the behavioural responses of deer to hunters. Specifically, I define these encounters as spatial-temporal contacts which represent co-occurrence of the two objects, or in this case hunters and deer. By definition, a contact occurs when a deer and a hunter are within a specified distance of one another at the same time. In defining contacts, I use a spatial distance threshold termed d_c , (Long *et al* 2014) to determine when a deer and hunter are deemed proximal to one another. Similarly, I use a time threshold to determine when a deer GPS point and hunter GPS point are deemed simultaneous termed t_c , (Long *et al* 2014). Requires consideration of in practice, the time threshold t_c should be directly related to the temporal properties of the GPS tracking data and is often chosen as $\frac{1}{2}$ the longest fix interval (Long *et al.*, 2014), in this case the longest fix interval was in the deer dataset at 8 minutes. An 8-minute fix interval represents a relatively fine scale of resolution for tracking data, allowing for studying of fine scale movement behaviour of deer (Pepin *et al* 2004). The distance threshold d_c is much more important, and therefore needs to be related to biologically relevant processes associated with the encounter between a hunter and a deer such as detectability by the deer.

To determine an appropriate distance threshold d_c for defining contact, I first considered information and knowledge on hunting activity. Specifically, it was deemed that in this region hunters regularly try to achieve a shooting distance of less than 200 yards

(Personal Communication; S. Webb 2020). Similarly, previous research has used a buffer distance of 100m when studying the interactions between hunters and white-tailed deer (Karns *et al.*, 2012), whilst other studies have found the zone of influence of human presence on anti-predator, or flight, behaviour in deer to be about 169 m (Stankowich and Coss, 2006). These reports suggest that an appropriate distance for studying deer response to human hunting, is likely within the range of 50 to 300m (Stankowich and Coss, 2006) when considering the multiple variables which influence anti predator behaviour in deer and hunter success in harvesting deer (Stankowich and Coss 2006). As this research is not focusing on alert distance, which would require behavioural observation, it was not needed to know at what distance the deer first perceives the hunter when deciding upon the spatial threshold. Additionally, the distance used could not be so great that it would define multiple contacts from different hunters within the study site. Therefore, I chose a distance threshold of $d_c = 150\text{m}$ to define contacts between hunters and deer.

Frequency distribution of contacts was also assessed by graphing the frequency of contacts at different distances (Fig 5) to confirm whether 150m was the correct threshold. The plot up to 500m did not show any clear distinction or cut off in distance at which contacts were grouped or dropped off. Therefore, I based the selection of the contact distance on the aforementioned literature sources.



3.5

Figure 5 A frequency plot of contact distances between deer and hunters at all distances below 500m using DCPlot function.

3.5 Analysing movement behaviours

Data was further processed to capture contacts into phases of a specified length using the same 8-minute temporal threshold as the GPS collar data. Context analysis was then completed which returned a data frame with variables of interest, in this instance step length (total, as opposed to straight line, distance moved between two GPS fixes). The first fix of a contact phase was chosen as the temporal instance for when a contact occurs.

Step length is the distance moved between two sequential GPS fixes, in this case 8 minutes, measured in metres (Calenge *et al.*, 2009). Movement was analysed in the 96 minutes before and 96 minutes after a contact in initial exploratory analysis, this window was chosen as previous literature suggests flight responses by white tailed deer in this area are likely temporally short (Marantz *et al.*, 2016).

The WildlifeDI package (Long, 2019) in R was used to identify contacts between deer and hunters which fell within the spatio-temporal thresholds chosen. The WildlifeDI package allowed me to do two important things. First, it allowed me to determine all instances where a deer was in contact with a hunter. Second, because these contacts often come in bursts (e.g., a deer may be in contact with a hunter for multiple consecutive GPS fixes) it allowed me to combine these sequences of contacts into single encounter events (the WildlifeDI package defines these as contact ‘phases’). I defined encounter events to be unique based on the temporal criteria of 1 hour, that is encounter events should be separated by a minimum of 1 hour in time to be considered a new unique encounter event.

Based on previous literature (Stankowich, 2008) the movement of the hunter was also calculated to determine the influence of this variable on the deer movement that results from contacts. The hunter associated with each contact was identified along with the time of the contact. Then using 4 fixes before and after the time of contact (~ 8-minute period) whether a hunter was moving or not was determined based on the cumulative distance moved by the hunter in that period. To account for noise in the hunter GPS data, it was deemed that any hunter who had moved less than 25m in that 8-minute period was not moving and any hunter that moved more than 25m in that period was moving (Fig 10). The hunters in the data set used a range of different methods, some stationary (such as hides and deer stands, and some moving (stalking). Therefore, this threshold based on the distribution of the data seen in Fig 10, accounted for these differences in movement by the hunters.

Table 2 Summary statistics of contacts generated by WildlifeDI showing the overall number of fixes for deer in the study, the number of contacts at $dc = 150m$, the number of phases within the contacts identified and summary statistics for each of those phases denoting the length, mean duration and median duration of phases.

Stat	Result
N fixes	270149
N contacts	808
N phases	247
Longest phase (secs)	15382
Mean phase (secs)	1226
Median phase (secs)	478.5
No. one fix phases	117

3.5.1 Data visualization

The desired variables were plotted to look at patterns in the data and display the individuals or grouped movement values for each 8-minute phase during these time periods. Using both line plots (Fig 7) and box and whisker plots (Fig 6) allows the interpretation of patterns across all individuals as well as inter-individual variation. I also compared to randomly selected fixes in the dataset (only when looking at step length), this is represented by the R value which is automatically generated by the WildlifeDI package. Preliminary exploration of the data allowed me to identify how many contacts were generated at the spatial and temporal thresholds chosen ($dc = 150$, $tc = 4*60$) and other summary statistics to better understand the data (Table 2).

After contacts were processed using conPhase and conProcess in WildlifeDI (Long 2019) variables of interest can be selected and plotted to look for patterns in the data. To do this I grouped responses to contacts (using box and whisker plots) and individual variation (using line plots) (Fig 6, 7). The step length variable was used as a proxy for speed, or the movement response rate, as the best representation of changes in movement pre and post contact. This makes sense given the literature on anti-predator responses mostly looks at flight and step length as a measure of distance travelled and speed at which it was travelled.

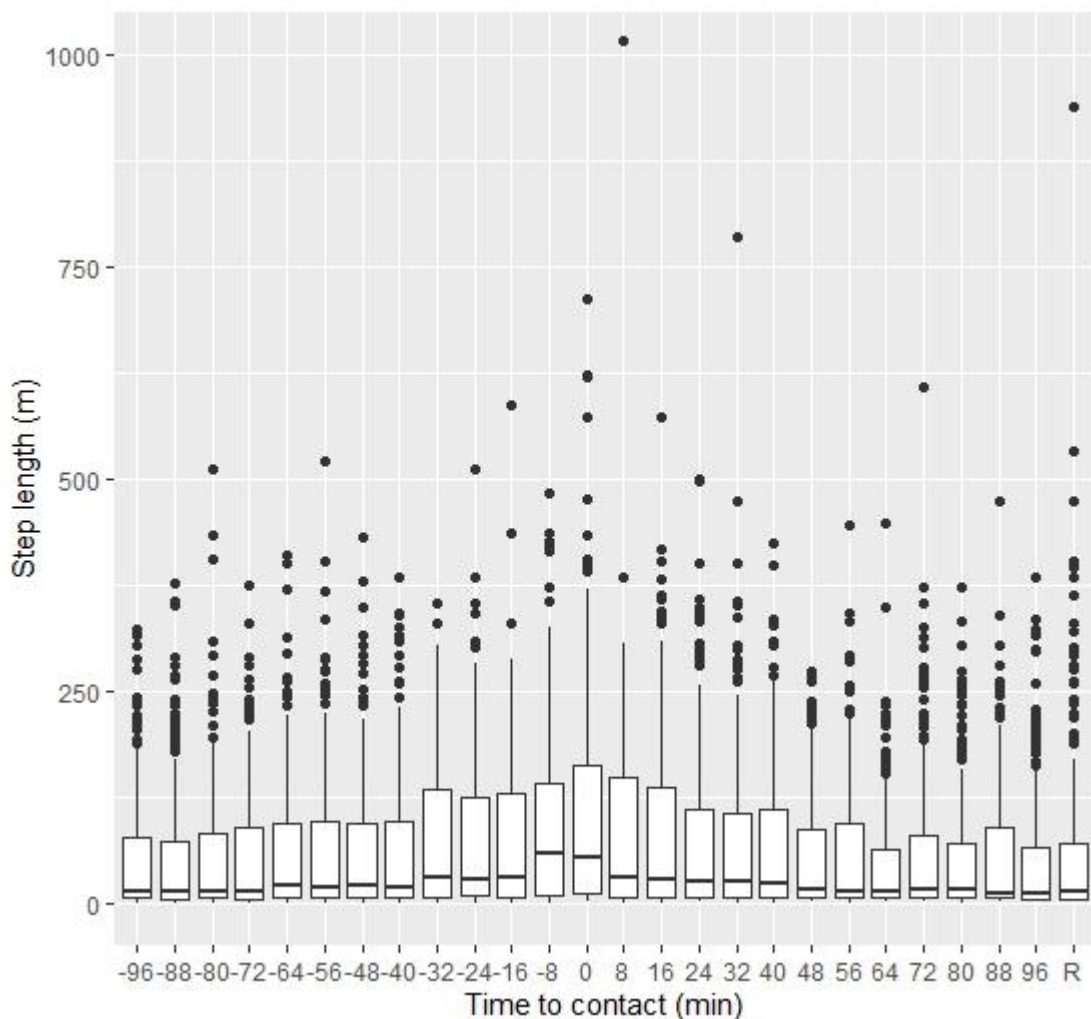


Figure 6 Box and whisker plot of step length (m) relative to temporal distance from contact (min) of white-tailed deer to human hunters using a contact distance of 150m (n= 247 contacts).

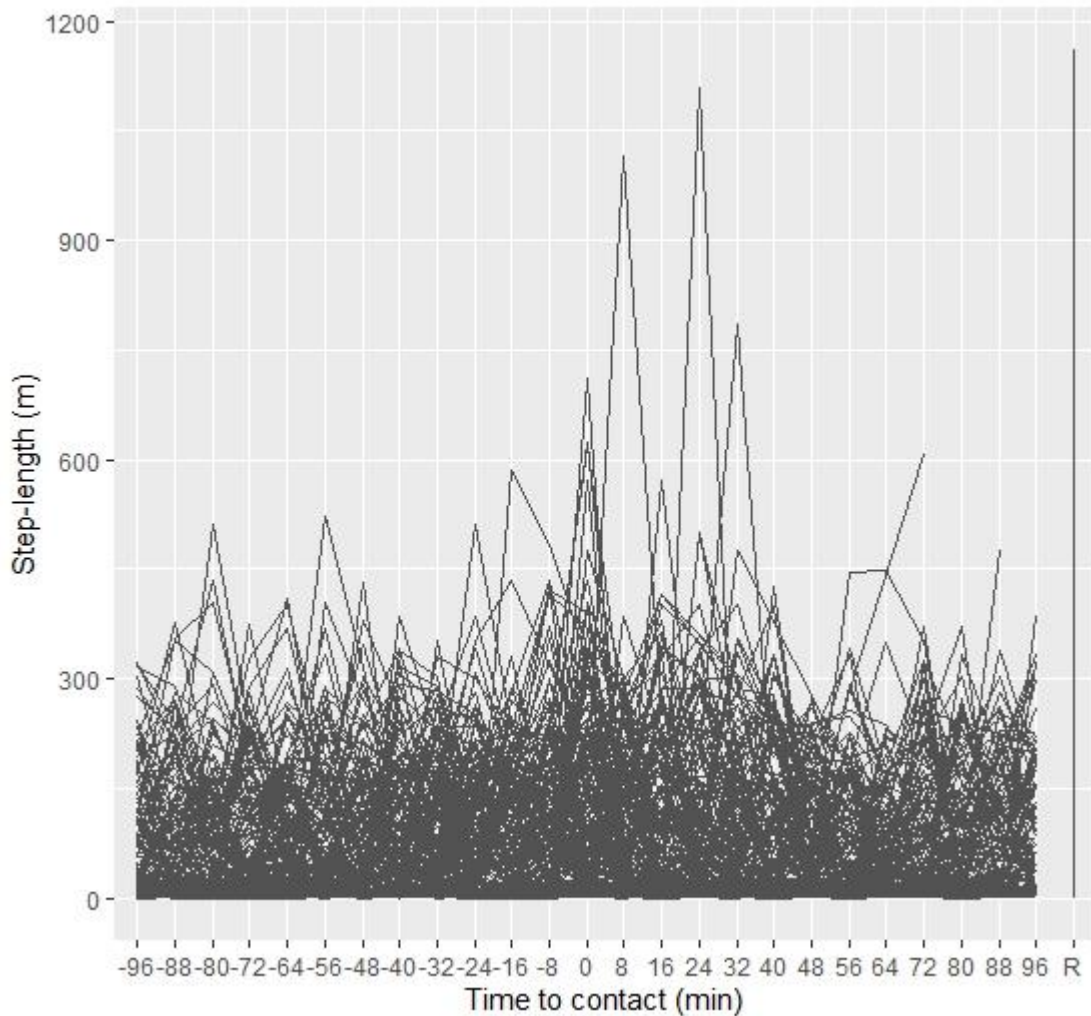


Figure 7 Step length (m) relative to temporal distance from contact (min) showing individual variation as a line plot (n = 247 contact events).

Step length, in Fig 7, shows some sharp peaks directly following contact for several individuals, however, there is continuous activity of the deer both before and after contact. There is a high amount of overlap between the individuals and no clear or definitive pattern in this plot with a high level of variation in response throughout the 96 minutes before and after.

The box and whisker plot (Fig 6) for step length shows, incremental increases until the greatest step length which is shown to be within 8 minutes of the contact, continuing to

decrease to 96 minutes post contact. The patterns seen here are similar to those in fig 7. These plots also show an R value to compare movement to randomly generated steps.

Once the movement variables were decided upon, additional variables were incorporated into the analysis data frame to allow the necessary analysis that would answer research question 2 and 3.

Whilst the descriptive techniques employed until this point were useful for identifying patterns and relationships in the data, statistical analysis was continued to establish which variables had a significant impact on the resulting movement of the deer. Regressions were also performed on the matched pairs.

3.6 RQ1 - Do encounters with human hunters alter the movement behaviour of white-tailed deer bucks?

To address RQ1, I used multiple analyses to complete comparative fine scale analysis of changes in behaviour before and after the contact at short temporal scale, behavioural response to the contact, matched pairs analysis to look at variable changes in contact vs no contact scenarios and finally Behavioural Change Point Analyses to look at the significance of these changes in movement compared to baseline movements.

3.6.1 Fine scale behaviour (Before/After Analysis)

For most of the movement analysis I used step-length as a proxy for movement. Step length is the linear distance travelled between two consecutive GPS points. Given that $\text{speed} = \text{distance}/\text{time}$, step length adequately represents changes in speed of movement by the deer with relatively high temporal resolution GPS tracking data with a fixed tracking interval (i.e., 8 minutes) as we have here. This is a commonly used proxy for movement in telemetry data (Simoneaux *et al.*, 2016).

I computed the step length this for each segment (pair of consecutive fixes) before and after a contact. I looked at step lengths before and after each contact for 96 minutes for a total of 192 minutes overall. This should capture any effects from detection of a hunter and, if present, flight behaviour (Avgar *et al.*, 2015; Prokopenko *et al.*, 2016).

I then used an unpaired t-test to compare whether the distribution in movement behaviour (step lengths) was significantly higher or lower during these segments before and after the contact to better understand the magnitude of any changes seen in movement. . To do this, the step lengths were grouped into before (B), contact (C) or after (A), resulting in categories B12 to A12 (Table 3). To further compare movement, I used the step length at 96 minutes before the contact, B12, as a reference point (Table 3) for the t-test. B12 was chosen, as it was seemingly distanced enough from the contact to not display any changes in step length size or median value. I then calculated the difference in step length from this reference for each subsequent step, to study if movement was significantly different compared with this pre-contact reference point. In doing this an assumption is being made that the reference step is truly not disturbed by other stimuli, however, we cannot confirm this. Thus, it is possible that the results could be skewed if the B12 step has a disturbance and is not representative of a true undisturbed state.

3.6.2 Behaviour response analysis (distance to contact, distance moved and hunter movement)

According to optimality models, an individual should flee once the costs of staying (death) become greater than the costs of fleeing (lost mating time, forage etc.) (Ydenberg and Dill 1986), this distance at which they do decide to move away from a threat is known as the Flight Initiation Distance (FID). To do so prematurely, however, would risk incurring unnecessary fitness costs so individuals will minimize this risk by staying put until the cost becomes too great to stay. There are a few factors which influence this calculation. A meta-analysis by Stankowich and Blumstein (2005) found characteristics of predators such as speed and directness influenced FID, as well as composition of prey (solo vs group), and environment such as distance to cover. Threat sensitivity hypothesis (Helfman, 1989) suggests prey may trade off anti-predator behaviour with other behaviours that increase fitness, such as eating, mating or resting, based on the perceived intensity of the threat. Whether a hunter is moving or not would be expected to affect the movement flight response of deer due to the optimal escape theory (Ydenberg and Dill, 1986) as a predator moving towards you, is more of a threat than a hunter that is still. Stankowich and Blumstein (2005) found that approach speed, directness and size of

predators influenced deer flight behaviour. Therefore, as the perceived threat becomes greater, the FID should increase. Closer hunters should be perceived as a greater threat and initiate flight vs staying put.

Using the sum of the step length I then calculated the cumulative distance moved post contact for 96 minutes. I used this total distance moved to look at the cumulative response of the bucks to the contacts and variables associated with the contacts. To calculate hunter movement, I created a threshold for movement in the step prior to the contact. A longer temporal window here captures the fact that deer may vary their movement flight response to hunters over a continued period after an encounter with a hunter. If hunter movement was greater than 25m, equivalent to 3.12m/min, this was coded as 1 and if the hunter moved less than 25m in the step before contact, they were coded as 0.

I completed a generalized linear mixed model (GLMM) using the lme4 package (Bates *et al.* 2015) and LMER Convenience Functions (Tremblay and Tucker, 2011) to test deer responses to predictor variables contact distance and hunter movement. The hypothesis was that smaller contact distances increase response of deer and threat intensity (hunter movement and distance of hunter) lead to greater response in bucks.

For these models distance moved post contact was the dependent variable, contact distance and hunter movement were used as fixed effects and deer ID was incorporated as a random effect.

I ran two models, first with only the contact distance as the covariate, and second both contact distance and hunter movement to assess combined affect, if any.

3.6.3 Matched pairs

Based on the preliminary results found in the descriptive graphs of the data, a matched pairs analysis was created to determine how great an effect the contacts had on the subsequent movement behaviour of the deer.

The matched pairs consisted of a comparison between the contact and days and times that were 24 hours before or after the contact. Analysis was done within the individual to

account for individual variations in response to hunter presence. This allows the comparison of contacts with somewhat random points in space and time.

. A matched pairs analysis individually pairs two sets of data and controls for all characteristics but the predictor variables, to see if the predictor variable significant influences the differences in the data (Ball *et al.*, 2001). Usually this is done with a study group and a control group, however, for this analysis individual bucks were paired with themselves before and after contact.

For each contact, I selected another GPS point from that individual 24 hours before the contact at the same time of day (I.e., within one hour of the time of the contact). If there was also a contact at this time in the day before, I selected a time the day before this (48 hours pre contact). This allows us to control for individual variation and changes in movement due to diurnal changes in activity as deer are crepuscular species. This created a dataset of matched pairs within individuals of contact (1) vs no contact (0). I was then able to look at what predictor variables influence the occurrence of contacts.

I calculated the movement pre contact as a sum of distance moved for 60 minutes before the contact to use a predictor variable. I then used a GLMM with a binomial response to perform a logistic regression between contact and deer movement 60-minutes pre contact, to assess whether deer that move more are observed more (Sage *et al.*, 1983), using movement as the fixed effect and deer ID as the random effect. The duration of 60 minutes was used as opposed to the earlier 96 minutes as, based on the results of those earlier plots and tests, the duration of response began to decrease at ~48 minutes post contact. As the anti-predator behaviour movements were the focus, the temporal window for the analysis was shortened to 60 minutes, so as not to include unnecessary step lengths.

3.6.4 Coarse Scale behaviour (BCPA analysis)

Finally, a Behavioural Change Point Analysis (BCPA) was performed to assess whether the movements and results seen in the previous analyses were significant to the overall movement patterns of the deer. To test if contacts were associated with different ‘behavioural change points’ that represent larger scale changes in behaviour, BCPA analysis was used (Gurarie, 2009). The changepoint analysis uses statistical likelihood to

identify points within trajectory data which are structural shifts in movement trajectories. It uses a combination of step length and turning angle to derive behavioural changes such as shifts from foraging to migration.

BCPA is dependent on parameters entered into the mode. For response time variable (X) I used $V_p = V \cos(\theta)$ where V is speed = displacement/time interval and θ is turning angle. I used a window size of 15 and a windowstep of 1. The window size is the temporal interval of analysis and was chosen because this encompassed two step lengths in our dataset, the windowstep represents the increments in which the analysis window moves forward. Larger windows are more robust but more coarse, smaller windows are more sensitive but more likely to generate spurious results. Therefore, I tried to use a window size that was small enough to analyse the data thoroughly and was relevant to our dataset and step length.

I then saved the changepoint breaks into a data frame to use in comparative analysis with matched pairs dataset. I compared the changepoints identified in the analysis with contacts and matched noncontacts to see if the contacts I identified using WildlifeDI, had a significant effect on the behaviour of deer based on behavioural state change. Specifically, I calculated the difference in time between the BCPA change points and observed contacts (and matched pairs)

The hypothesis being that true contacts are closely associated in time with globally significant behavioural change points.

I then completed another GLMM to compare these statistically, using changepoints as the dependent variable and contact as the independent with deer ID as random effects.

3.7 RQ2 - Do habitat/landscape attributes mediate the movement behavior (e.g., flight response) of white-tailed deer bucks following encounters with hunters?

To address RQ2 I looked at whether habitat variables influenced the number of contacts seen or the post contact movement behaviour. Habitat is thought to be one of the most influential variables of deer movement (Simoneaux *et al.*, 2016)

3.7.1 Matched Pairs

Firstly, to assess whether habitat variables influenced the probability of a contact I used the matched pairs data to compare contacts with habitat variables. I used the following variables: landcover (Table 1), slope, road distance and treatment (hunter pressure). This is in line with other papers on hunter success and space use and deer space use during hunting season (Cooper *et al.*, 2002; Rowland *et al.*, 2021; Swenson, 1982). I then completed a GLMM with a binomial response (0 = match pair, 1 = contact).

3.7.2 Movement Behaviour

To see how much movement there was between habitat types at contact and post contact I created a transition plot using habitat at time of contact and 30 minutes post contact. The threshold of 30 minutes was used, based on analysis in 3.6.2, and the results (section 4.1.1.1) which suggest flights are short lived and their durations are usually short, I wanted to identify which habitat they were fleeing to/using for cover. Unlike the distance moved in 60 minutes, it was not necessary for their movement to return to a baseline level. Therefore, the shorter duration was used to capture the habitat use at the time of contact and directly following flight. Using the hypothesis that deer who had contacts in open habitats would move to more vegetated habitats.

After testing for association of habitat variables with probability of contact and looking at the transition plot. A GLMM was performed to test the association of contact distance and habitat variables, as visibility of deer and hunter success is closely associated with habitat variables, with more open habitats having a positive correlation to observations and successful harvest (Lebel *et al.*, 2012).

Given that deer use forested habitats as cover from predators (Vercauteren and Hygnstrom, 2004; Riley *et al.*, 2003) and visibility for hunters would be better in open habitats, the hypothesis is that deer who have contacts in open habitats would move farther post contact than deer in other habitats because greater threat = greater flight initiation distance (Stankowich and Coss, 2007).

A GLMM was completed for movement post contact (sum of distance) and habitat types post contact to test the relationship between movement and cover type post flight (Meier, 2021; Henderson *et al.*, 2020; Stankowich and Coss, 2007). If deer are seeking cover from hunters, it would be expected that post contact there will be a higher use of covered habitats vs open habitats.

3.8 RQ3 - Does the age of bucks influence the probability of encounters occurring and/or response to encounters with hunters?

The literature shows that deer have the ability to learn (Jakopak *et al.*, 2019; Lewis *et al.*, 2021; Merkel *et al.*, 2019; Ranc *et al.*, 2021; Wolf *et al.*, 2009; Gillingham and Bunnell, 1989) over time and use spatial memory to migrate and find food resources. To have survived harvest or predation as a young buck and survive to older age classes, bucks presumably have employed successful anti-predator strategies. These could be using different habitats to avoid predators altogether or different flight strategies. Additionally, hunters often select for older bucks through selection of larger antlers (Schoenbeck and Peterson, 2014). So, the older a buck is, the better their evasion strategies must be.

To test this, I compared the age of bucks to their contact behaviour. Bucks were aged by tooth replacement and wear at age of capture (Little, 2011).

Firstly, to understand if age impacted the likelihood of a contact occurring, when plotted there did not appear to be significant variation, I completed a GLMM with a binomial response (0 = no contact, 1 = contact). This was not based on the matched pairs dataset but the raw data with contacts coded as a 0 or 1.

After looking at the likelihood of contact, I tested the contact distance and age to identify if there was a relationship between age of buck and threat perception. It would be expected that if older bucks had learnt to identify danger more quickly, their contact distances would be greater due to an increased flight initiation distance.

I then used a GLMM to look at distance travelled after contact. For each individual, I calculated the cumulative distance as the sum of the step lengths in the time period of increased movement following a contact (i.e., 30 minutes after a contact) and used this as

the dependent variable in the model, deer ID was used as a random effect, deer age was a fixed effect. I then ran the model again, including landcover, hunter movement, deer movement post contact.

4 Results

4.1 RQ1 - Do encounters with human hunters alter the movement behaviour of white-tailed deer bucks?

4.1.1 Fine Scale Behavior (Before/After analysis)

Step lengths leading up to and following contact with hunters at 150m were generated (Fig 8) shows movement is increased (based on the median) from 32 minutes pre contact and increased movement persists until 40 minutes post contact. Prior to 32 minutes before the contact the median step length is low and there is little variation up until this point where it increases. At 48 minutes after the contact median step length decreases and remains low for the remainder of the plot. This plot also highlights that the step lengths show a fairly high level of variation between individuals at each step, and the upper quartile values are more distant from the median than the lower quartiles, suggesting variation is greater in larger step lengths.

T test performed on this data to test significance of these differences found a significant increase in movement from about ~40 minutes before (B5) to 24 minutes after (A3) the contact in the step lengths (Table 3).

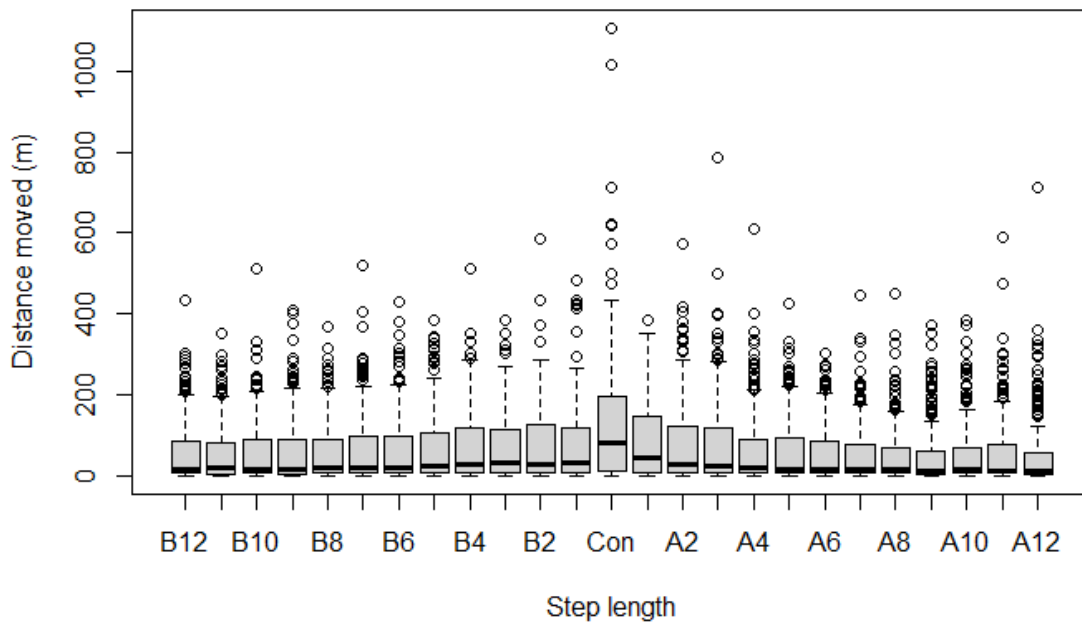


Figure 8 Step lengths of deer movement, relative to time of contact with hunters after grouping into before and after categories for 96 minutes pre and post contact ($n = 247$ contact events). The label B12 refers to 96 minutes before the contact, while the label A12 refers to 96 minutes after contact. Each increment in these labels represents an 8 minute time increment relative to the contact event.

Table 3 Times before (negative values) and after (positive values) contact events that exhibited significantly higher (using a t-test; $n=247$ contact events) movement rates relative to the comparison period. These periods refer to the periods B5 to A3 in **Figure 8**.

Time To contact (min)	P-value
-40	0.0157
-32	0.00884
-24	0.0126
-16	0.0108

-8	0.00352
0	p < 0.001
8	0.00002
16	0.000387
24	0.00530

4.1.2 Behaviour Response (distance to contact/hunter movement)

Contact distance showed a negative association ($p = 0.024$) with distance moved by deer post contact (Table 4). The coefficient for contact distance was -2.601 which suggests that for every meter closer a hunter gets, deer move 2.601 meters more in response to a contact.

The GLMM results show that there is a significant relationship between contact distance and distance travelled post contact at the $\alpha = 0.05$ level. The negative sign of the estimate suggests that contacts in closer proximity with hunters are associated with greater movement responses by the deer.

Table 4 GLMM results of model using distance moved by bucks' post contact as the response variable and contact distance with the hunter (in m) as the independent variable ($n = 105$ contact events).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	810.611	100.632	171.726	8.055	0.000
Contact distance to hunter	-2.061	0.906	233.134	-2.275	0.024

Deer movement shows a strong cluster when hunter movement is less than 25m in the step before contact (Fig 10). There is also some variation in post contact distance travelled by bucks' dependent on whether the hunter is moving or not (Fig 11).

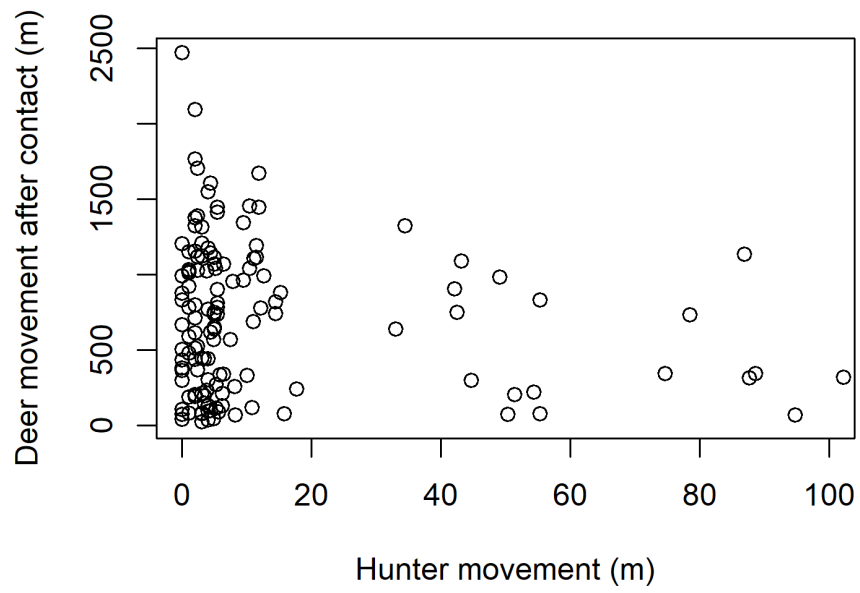


Figure 9 Distance moved for 60 minutes by hunters (m) vs deer (m) post contact at $dc = 150m$ ($n = 247$ contact events).

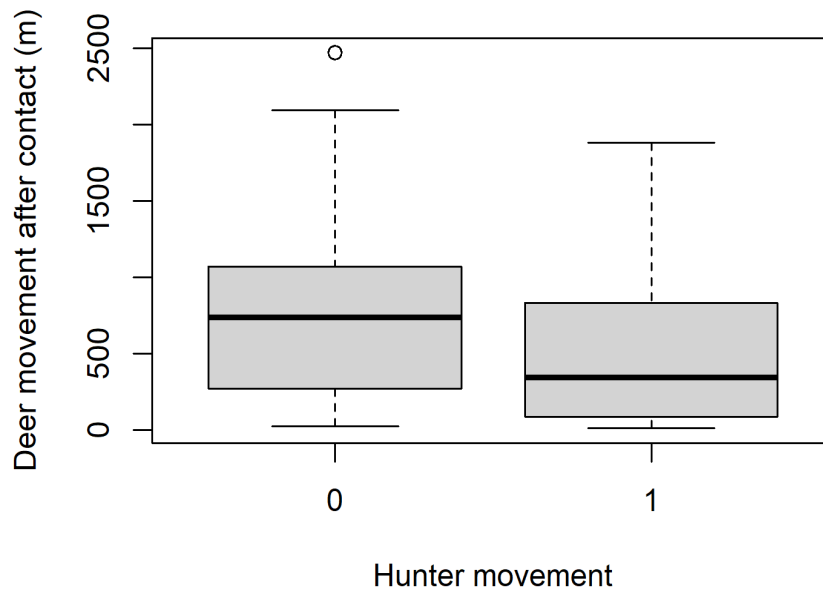


Figure 10 Deer movement post contact, for 60 minutes, compared with hunter movement as a binary moving (1) or not moving (0) based on 25m movement threshold (hunters moving greater than 25m were considered moving).

The results of a univariate GLMM based on hunter movement without the inclusion of contact distance (Table 5) show a significant relationship at the $\alpha = 0.05$ level between hunter movement and distance moved by bucks' post contact, based on the 25m threshold of hunter moving or not moving. The negative coefficient represents a negative relationship between the two variables, showing when hunters are moving at time of contact, deer show decreased movement post contact then when hunters are still.

Table 5 Results of a univariate GLMM using distance moved by bucks' post contact as the response variable and hunter movement (binary; 0 = not moving, 1 = moving) as the independent variable (n = 105 contact events).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	718.376	58.159	45.687	12.352	0.000
Hunter Moving	-185.821	62.077	238.043	-2.993	0.003

When the GLMM is repeated for hunter movement with the raw distances moved by hunters instead of the 25m threshold the results are as follows (Table 6). There is no significant relationship shown between the movement of the hunter and the distance travelled by bucks' post contact at the $\alpha = 0.05$ level. This suggests that whether the hunter is moving is more likely to influence deer behaviour than the speed at which the hunter is moving.

Table 6 Results of a univariate GLMM using distance moved by bucks' post contact as the response variable and hunter movement (in m) as the independent variable (n = 105 contact events)

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	638.832	53.109	22.658	12.029	0.000
Hunter Moving	-0.044	0.034	241.660	-1.294	0.197

To look at the combined effect of both contact distance and hunter movement, a final GLMM (Table 7) shows a significant relationship between contact distance, but not hunter movement at the $\alpha = 0.05$ level. The contact distance is still showing a negative relationship with deer movement. The hunter moving coefficient is also still negative, but is no longer significant, suggesting that contact distance more than whether the hunter is moving influences deer movement response post-contact.

Table 7 Results of a GLMM using distance moved by bucks' post contact as the response variable and hunter movement (binary; 0 = not moving, 1 = moving) and contact distance to the hunter (in m) as the independent variables (n = 105 contact events).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	1036.393	190.147	101.998	5.451	0.000
Contact distance	-3.406	1.638	95.832	-2.079	0.040
Hunter Moving	-99.300	88.244	97.299	-1.125	0.263

4.1.3 Matched Pairs

Initial plot (Fig 12) of how much deer move before contact and contact or no contact using the matched pairs showed deer with contacts moved less prior to contacts relative to the matched pairs the day before.

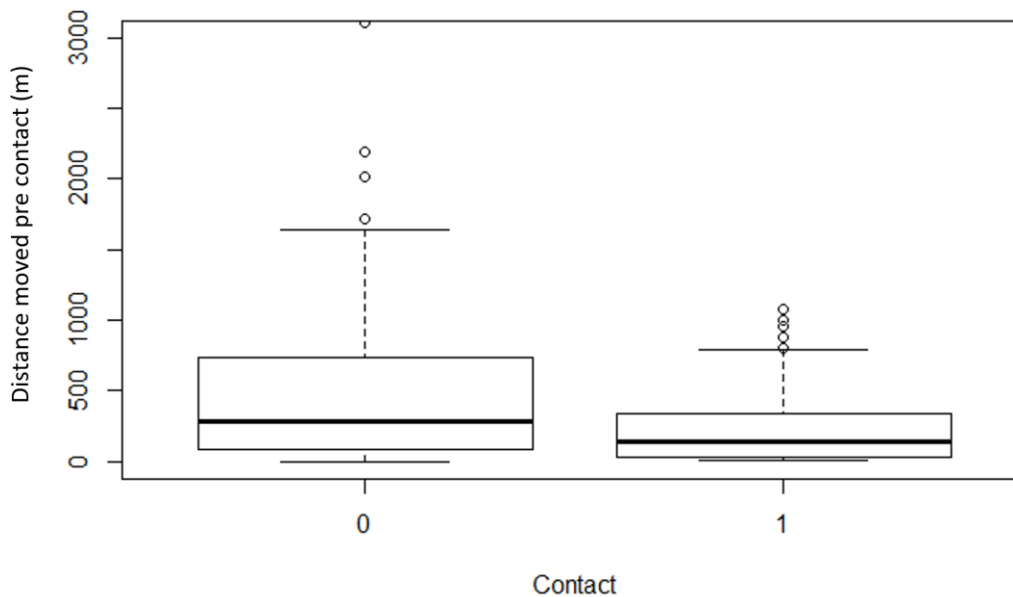


Figure 11 Box and whisker plot of distance moved pre contact and whether a contact occurred or not based on matched pairs at dc = 150m (n = 247 contact events)

Results of a GLMM with binomial response contact (1) or no contact (0) (Table 8) show there is no significant relationship between the distance travelled pre contact and likelihood a contact occurs at the $\alpha = 0.05$ level.

Table 8 Results of a binomial GLMM using a response of true contact (1) and matched pair (0) from matched pairs analysis as the response variable and distance the buck moved for XX minutes before the contact (or matched pair) event as the independent variable (n = 492) .

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.022	0.101	0.215	0.830
Dist before	-0.000	0.000	-0.467	0.640

4.1.4 Course Scale Behaviour (BCPA analysis)

The BCPA changepoints that were compared to the matched pairs contact (1) no contact (0) after analysis using a GLMM with a binomial response (Table 9) did not show a significant relationship at the $\alpha = 0.05$ level. These results suggest that there is no significant difference in the agreement of the global BCPA changepoints with the true contacts (compared to the matched pairs) with a P value = 0.054.

Table 9 Results of a GLMM using distance in time (minutes) between BCPA change points and contact events. The independent variable was a binomial indicator of whether the event was a true contact event (coded as 1) or a matched pairs (coded as 0) (n = 492)

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	19.958	1.199	71.464	16.649	0.000
Contact	-3.086	1.599	477.314	-1.929	0.054

4.2 RQ2 - Do habitat/landscape attributes mediate the movement behavior (e.g., flight response) of white-tailed deer bucks following encounters with hunters?

4.2.1 Matched Pairs

Table (10) shows the GLMM results using binomial response for matched pairs compared to habitat variables and other covariates. Each habitat category is listed in addition to slope, road distance and hunting pressure treatments. Variables which generated a significant response to contacts are: road distance and high hunting pressure. These results suggest that contacts occur closer to roads than non-contacts, and that contacts occur more commonly in areas with higher treatments relative to the no treatment areas.

Table 10 Results of a binomial GLMM using a response of true contact (1) and matched pair (0) from matched pairs analysis as the response variable and habitat variables, topography, road distance and hunter pressure treatments as independent variables (n = 492)

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.064	5.309e-01	-2.003	0.045
Mixed	0.012	2.636e-01	0.045	0.964
Forest	0.353	2.557e-01	1.379	0.168
Road	-20.452	2.265e+04	-0.000	0.999
Pond	0.646	1.589e+00	0.406	0.685
Riparian	0.377	2.840e-01	1.326	0.185
Slope	0.008	3.242e-02	0.238	0.812
Road_Dist	-0.000	1.726e-04	-2.075	0.038
TreatHigh	1.361	4.839e-01	2.813	0.005
TreatLow	1.425	5.129e-01	2.778	0.005
TreatOffProp	-0.265	6.555e-01	-0.405	0.686

4.2.2 Movement Behaviour

Based on plots of habitat at time of contact (Fig 13) and 30 minutes post contact (Fig 14) some change can be seen between habitat types. The transition plot (Fig 15) shows

minimal change in the overall distribution of each habitat before and after contact. It does show, however, a noticeable amount of movement between habitat categories. The proportion of contacts which led to a change in habitat vs no change in habitat was 47%. So, in almost half of contacts bucks changed habitat type following contacts with hunters.

The most contacts occurred in the forested habitat type followed by field, with mixed and riparian being almost indiscernible in frequency differences.

30 minutes post contact there is some change in the distribution of habitats but forested retains the highest frequency, followed by field as at the time of contact with the two highest frequencies. There is now a small discernible difference between mixed and riparian with mixed having a slightly increased frequency over riparian habitat. (Fig 14)

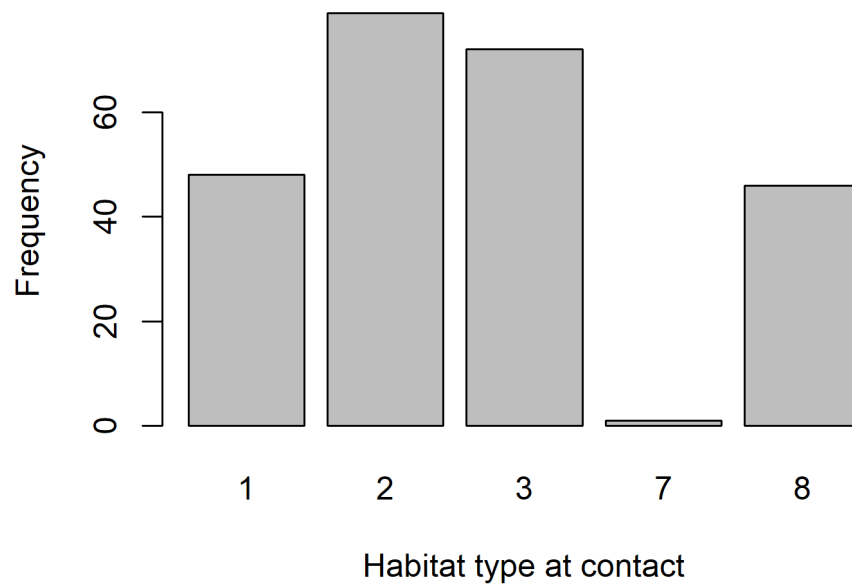


Figure 12 Habitat types at time of contact by frequency at contact where 1 = Mixed, 2 = Forest, 3 = Field, 7 = Non habitat and 8 = Riparian habitat. See Table 1 for further definitions of habitat types.

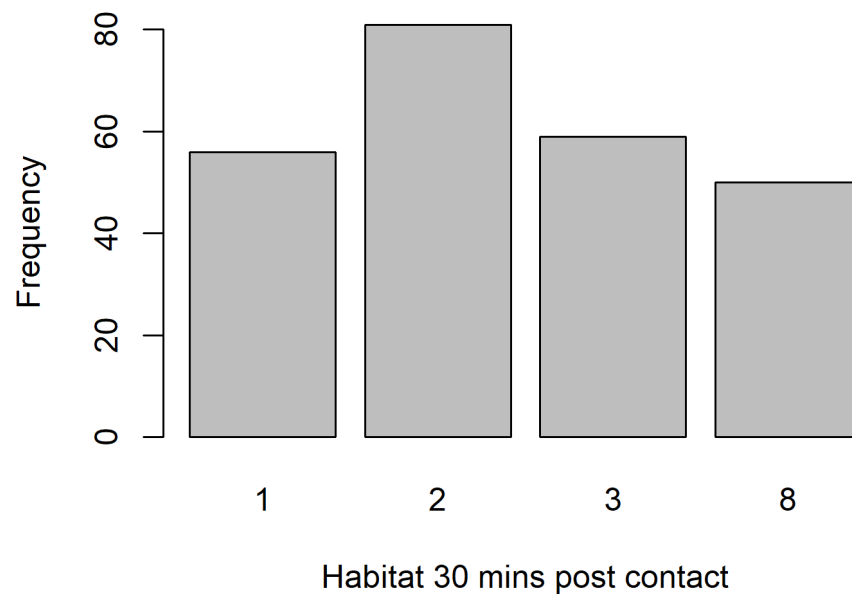


Figure 13 Habitat use by frequency 30 minutes post contact where 1 = Mixed, 2 = Forest, 3 = Field, 7 = Non habitat and 8 = Riparian habitat. See Table 1 for further definitions of habitat types.

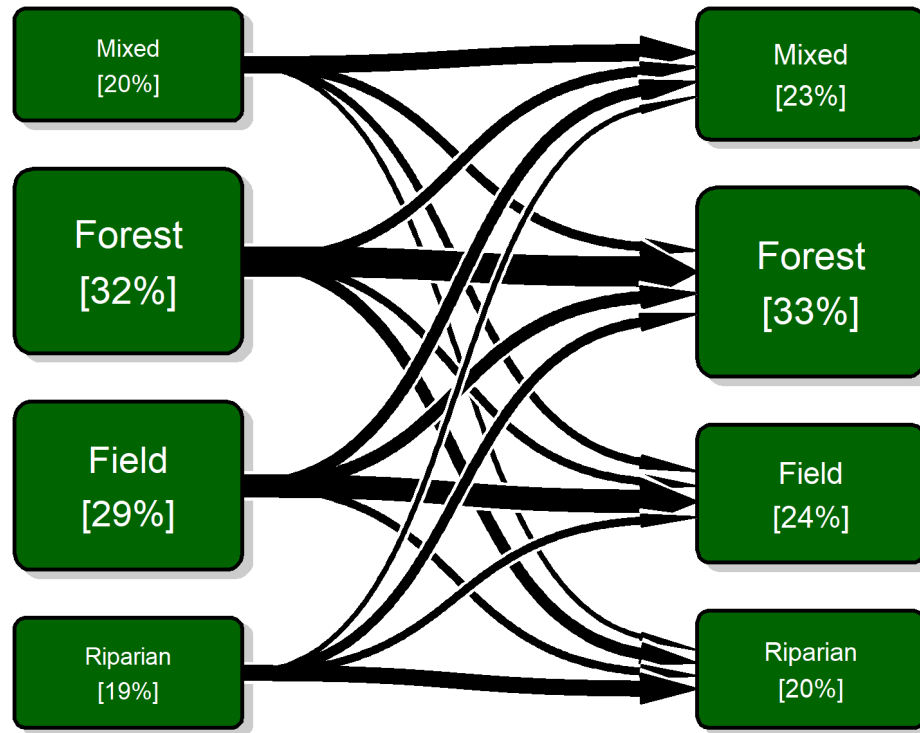


Figure 14 Transition plot showing differences in habitat use at time of contact vs 30 minutes post contact and change between habitat categories.

GLMM on contact distance and habitats (Table 11) showed no significant relationship between different habitat types and the distances at which contacts occurred. There are no significant relationships between habitat types and contact distance at which contact occurred at the $\alpha = 0.05$ level.

Table 11 Results of a GLMM using contact distance from hunter (in m) as response variable and habitat variables as the response variable (n = 105).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	137.233	25.984	100	5.281	0.000
Mixed	-9.144	26.896	100	-0.339	0.734
Forest	-28.939	26.278	100	-1.101	0.273
Field	-24.932	26.479	100	-0.941	0.349
Riparian	-27.911	26.626	100	-1.048	0.297

Results of a GLMM for distance moved post contact which incorporated landcover both at contact and post contact (Table 12), in addition to hunter movement, contact distance, and age only one out of five predictor variables show significance at the $\alpha = 0.05$ level.. All other variables were not significant.

Table 12 Results of a GLMM using distance moved post contact (in m) as the response variable and landcover, hunter movement, contact distance and age as the independent variables (n = 105) .

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	1357.908	261.992	40.800	5.183	0.000
Contact distance	-3.042	1.654	95.656	-1.839	0.068
Hunter Move	-127.352	89.083	97.534	-1.429	0.156
Landcover at contact	-5.139	19.078	97.872	-0.269	0.788
Age	-120.709	54.322	17.544	-2.222	0.039
Landcover post contact	19.442	17.628	98.521	1.103	0.273

When the GLMM was repeated and only landcover at contact and landcover post contact were retained in the model (Table 13), a significant relationship between landcover post contact and distance moved that is significant at the $\alpha = 0.01$ level can now be seen. Landcover at the time of contact continues to show no significant relationship.

Table 13 Results of a GLMM using distance moved post contact (in m) as the response variable and landcover at the contact and post contact as independent variables (n = 105).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	539.679	73.264	58.954	7.366	0.000
Landcover at contact	-14.468	14.964	241.331	-0.967	0.335
Landcover post contact	34.219	12.918	237.123	2.649	0.009

To further delineate the differences in movement post contact due to habitat (based on the results of Table 13), if any, the landcover was split into the habitats from the raster as factors to use in the GLMM (Table 14). There is no significant relationship between any of the habitat categories and deer movement post contact at the $\alpha = 0.05$ level. Standard error values for these habitat values are high in comparison to those in tables 12 and 13.

Table 14 GLMM testing relationship between distance moved post contact as the response variable and habitat type post contact as the independent variable (n = 23 105).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	335.698	494.983	237.611	0.678	0.498
Mixed	185.687	498.086	234.913	0.373	0.709
Forest	288.794	497.328	235.996	0.581	0.562
Field	356.272	498.023	236.239	0.715	0.475
Riparian	267.169	500.053	236.387	0.534	0.594

4.3 RQ3 - Does the age of bucks influence the probability of encounters occurring and/or response to encounters with hunters?

The graphs of frequency and age show that there is a skewed age distribution in the dataset that favours young bucks. Frequencies of different ages remain largely the same between all bucks (Fig 16) and those that exhibit a contact (Fig 17) with the exception of 8.5-year-olds who are not represented at all in the contact dataset.

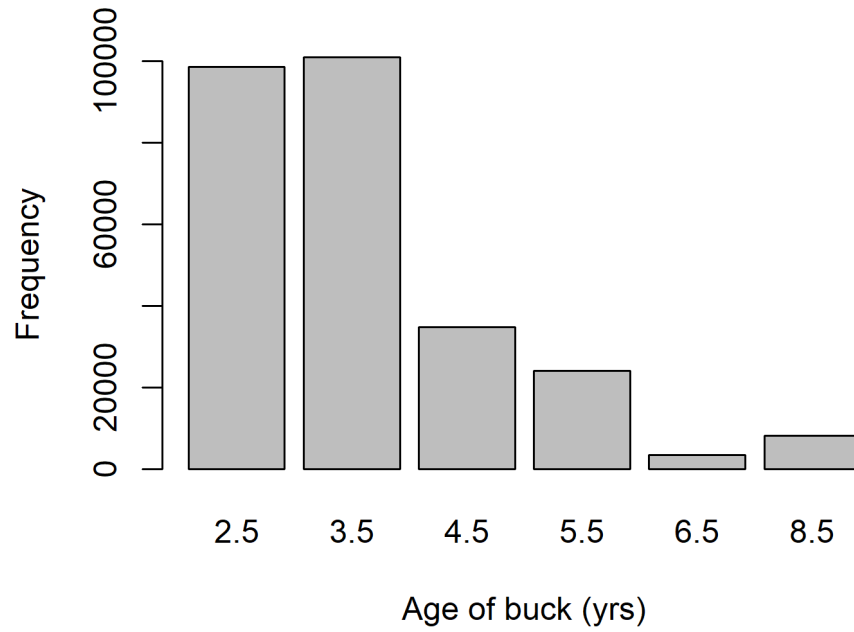


Figure 15 Frequency of all GPS fixes by buck ages

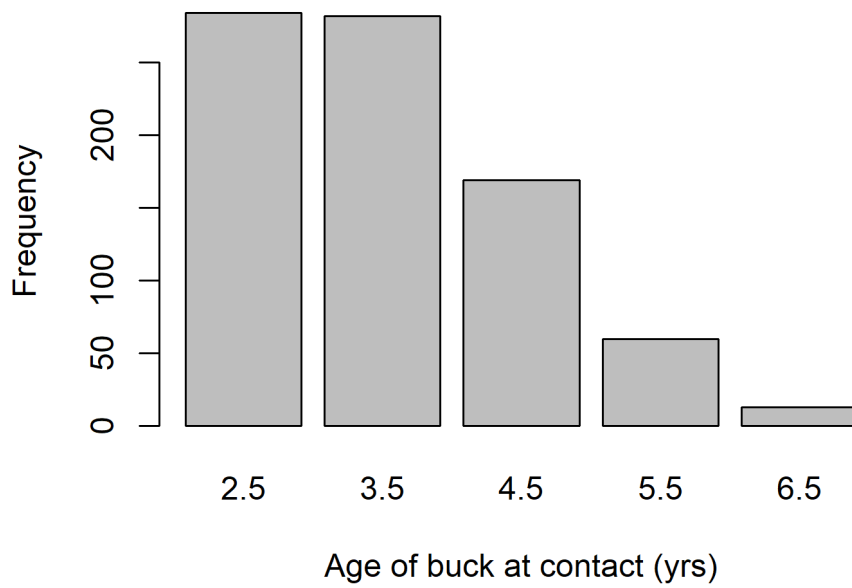


Figure 16 Frequency of GPS fixes by bucks in the contact subset of events 150m contact threshold

Results of the GLMM for age and probability of contact (Table 15) showed there was no significant relationship between age and likelihood of a contact. Therefore, it does not seem that older bucks have less contacts than younger bucks based on this data.

Table 15 Results of a univariate GLMM using a binomial response between contact (1) or no contact (0) and age of buck.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-6.487	0.583	-11.135	0.000
Age	-0.031	0.142	-0.217	0.828

Next, the relationship between contact distance and age was tested using a univariate GLMM. Results did not show a significant relationship at the $\alpha = 0.05$ level (Table 16).

Table 16 GLMM using contact distance as the response variable and age of buck as the independent variable (n = 105).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	107.378	9.425	103	11.392	0.000
Age	1.487	2.685	103	0.554	0.581

The results of the GLMM to test the relationship between distance moved post contact and age of buck showed a non-significant correlation (Table 17) at the $\alpha = 0.05$ level. This was the strongest relationship for age out of the contact probability, contact distance and post contact response.

Table 17 GLMM using distance travelled post contact (in m) as the response variable and age of buck as the independent variable (n = 105).

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	907.569	172.589	19.805	5.259	0.000
Age	-81.248	46.435	20.779	-1.749	0.094

Finally, in the earlier multivariate GLMM (Table 12) for movement behaviour post contact, age did show a significant relationship $P = 0.03$. This univariate GLMM relationship is therefore supportive of the result in the multivariate movement analysis.

5 Discussion

5.1 Movement

The results show that dynamic interactions with hunters do elicit a movement response from bucks at our study site. The significant movement around contact events from 40 minutes pre contact to 24 minutes post contact (32 minutes if inclusive of the step containing contact) shows that deer do initiate a flight response to hunters at a population level. The increase in movement pre contact, in advance of contacts, may be for several reasons. Meier (2021) found deer that moved more had increased observability to hunters at this study site. Thus, if deer are already moving when a contact occurs, the step lengths would be increased prior to the contact itself.

This increase in movement before contacts, as defined by WildlifeDI, could be the result of differences between temporal scales at which contact distance is calculated compared to those of anti-predator behaviour exhibited by bucks. Sutton and O'Dwyer (2018) defined the start of an encounter as the point at which deer first detect a threat known as alert distance (AD), therefore the bucks in this study may have detected the presence of hunters long before the 150m threshold and initiated movement prior to what was defined as a contact. Additionally, flight initiation distance (FID), which is closely linked to AD may have been reached earlier than the 150m threshold, especially if the hunter was moving at the time of contact. Stankowich and Coss (2007) found that greater flight response was initiated with greater FID, linked to the perceived threat level of the predator by the deer. A moving hunter is a greater threat and therefore flight would be initiated at a greater distance, so it is possible in this circumstance that deer would start moving before the hunter came within 150m of them. Post contact, deer only showed a significant response for 30 minutes. Stankowich and Coss (2007) found that deer on average fled $105 \pm 12\text{m}$ after disturbance with hunters. Based on our results in Fig 8, the mean movement in the step lengths Con + A1 + A2 and A3 would be approximately 100m of movement in those 32 minutes. This is in line with the findings of Stankowich and Coss (2007). For some of the deer in our study, 105m would be covered in one step length, and Fig 8 shows large variation above the mean value for step length at contact suggesting that this is the case for many of the deer in our study area.

Contact distance showed a strong and significant relationship with post contact flight distance ($\alpha = 0.05$ level). Specifically, post contact flight distance was negatively associated with the distance between the hunter and the deer at the time of the contact, which means that deer move greater distances when hunters are closer to them at the time of contact. These results confirm our hypothesis that greater risk results in a greater flight response by the deer. This is in keeping with previous literature that greater risk elicits greater response (Stankowich and Coss, 2007; Stankowich 2008) however, this is contrary to the findings of Stankowich and Coss (2007) where flight distance had a positive relationship with FID, that is, deer which fled at greater distances from the predator had longer flight distances. Although these findings appear to contradict each other, in the context of optimality theory both results align in that greater risk elicits a larger flight response. If the threat is great then deer may flee sooner as in Stankowich and Coss (2007) or if the threat is imminent, and the deer therefore have no choice but to flee, they would also be expected to elicit a large response. Again, the difference in methods may also account for some of the difference seen here as FID and contact distance are not the same metric. As was seen in the step length analysis, there are increases prior to what I identified at contacts, suggesting that FID may have already been met prior to contact with hunters.

The benefit to risk trade-off would also be expected to be mediated by the distance to cover from predators. Prey may stay in place for longer if they are close to cover, then prey that are farther from cover at the time of an encounter. This allows them to optimize gains until they have fully assessed the risk that is present (Sutton and O'Dwyer, 2018). Thus, in addition to looking at FID and contact distance, a model that also incorporated distance to cover would elucidate the decision-making process on when to flee and how much of a threat the predator poses. There is some support for this in the findings of Stankowich and Coss (2007) where they found that deer in habitats composed of only grass had greater flight distance compared to other habitat types. Similarly, (Cooper and Frederick, 2010; Hemmi and Pfeil, 2010) found that the strongest threats provoke the earliest response.

Furthermore, the behaviour of the hunter is likely to add to calculation of perceived risk (Stankowich and Coss (2007); Sutton and O'Dwyer (2018)) by deer and therefore, the FID or contact distance flight takes place at. Our results showed a strong correlation between hunter movement and deer movement post contact ($P = 0.003$) with a negative coefficient. This result is somewhat unexpected, as it means that when hunters are moving deer tend to move less post contact than when hunters are still. Previous literature found the opposite, that hunters that were moving posed a greater threat and therefore a greater flight distance. It is likely that this result is mediated by the habitat in which the contact takes place, and therefore distance to cover. Meier (2021) found that the majority of deer observations by hunters were in forested habitats within our study area, if deer are already in cover habitat, then they will not have to travel as far to seek cover from hunters.

Whilst this result is surprising, Stankowich and Coss (2006) found that predator behaviour, including speed, angle of approach, directness of gaze and possession of a mock gun influenced the resulting flight behaviour of deer. Therefore, this result warrants further investigation regarding additional variables of the threat (Sutton and O'Dwyer, 2018).

When hunter movement was calculated using the raw hunter movement speeds there is no significance. This suggests there may be a threshold relationship between hunter approach and movement by deer, instead of a direct correlation between speed and flight, linked to deer perception, Karns *et al.*, (2012) found limited response to hunting pressure in their study but note that it was far below the previously reported behavioral response threshold Root *et al.* (1988) of 0.45 hours/ha/day, as were the hunting pressures in this study when averaged (Little, 2011). Alternatively, the hunter simply moving vs not moving may be enough to elicit the perception of a threat by the deer. This could be important for understanding how managers can best utilize hunting as a tool for deer populations, as they would then be able to implement hunting methods that lead to greater response by deer (e.g., tree stand vs stalking). Other models suggest that not only movement is important but whether this movement is sustained over the approach of the predator (Sutton and O'Dwyer 2018) which may explain why speed does not show a relationship,

but the threshold approach to movement does. This presence of threshold for anti-predator behaviour in response to hunting pressure has also been suggested in other studies (Little *et al.*, 2016; Neumann *et al.*, 2008).

When the model combines both movement and contact distance, however, contact distance had a more significant relationship. Which suggests the distance to the threat is more important than the speed or movement of the hunter, in whether deer flee or not in this dataset. This is in keeping with the finding that closer contact distances initiate greater flight distances.

Meier (2021) found that deer that moved more were observed more by hunters, this is in keeping with previous literature that observability is linked to the movement behaviour of individuals (Little *et al.*, (2014); Little *et al.*, (2016); Marantz *et al.*, (2016)). Our initial descriptive analysis of this relationship was contradictory to previous findings and showed deer with contacts moved less before contact compared to their matched pairs. When tested by GLMM, however, there was no significant relationship between movement before contact and whether a contact occurred. Therefore, our results neither agree nor disagree with previous findings, and they may be explained by changes in habitat use by hunters, following changes in habitat use by deer as Meier (2021) found that most observations between hunters and deer took place in forested habitats. Deer typically use forested habitats for bedding and cover, thus their movement in forested habitats would be less than in non-forested habitats. It was found by previous studies (Little *et al.*, 2016; Marantz *et al.*, 2016) that during the rut, bucks increase movement in a contracted home range. Thus, it is possible that bucks are moving more but not being observed as often, due to contraction of home range to more covered habitats as is suggested by Meier (2021). To further test this, a study design that encompassed the identification of contacts in an area with no hunting pressure, would be an adequate comparison as contacts were only calculated for deer and hunters within units that had low or high hunting pressure. Overall, this result would suggest that in our dataset, it is not the movement of the bucks' pre-contact that is driving contact events with hunters but another variable, or combination of variables.

It has been established that it is possible to identify flight responses and changes in behaviour of bucks responding to contacts with hunters using GPS data and WildlifeDI. The BCPA analysis was intended to analyse how closely the changes in movement observed using the WildlifeDI analysis, were aligned with changepoints as identified by the BCPA change of state analysis. Whilst there was no significant relationship, at the $\alpha = 0.05$ level, identified between the two the P value of 0.054 suggests that with greater parameter selection, it may be possible to match BCPA changepoints to contacts as identified using WildlifeDI.

In the model I used both speed and turning angle for the BCPA parameters, however, in our analysis responding to contacts, I only used step length and excluded turning angle. Therefore, this could be due to slight differences in the two parameters that were used, one being combined and one being just step length (as a proxy for speed). The adjustment of the K value (and therefore sensitivity of the BCPA) may have been appropriate if further tests were carried out. This is promising for future capabilities of using movement tracks and GPS data to identify and quantify disturbance to wildlife and behaviour change in response to anthropogenic disturbance.

Overall, research question 1 can be answered in that encounters with hunters do alter the movement behaviour of deer and these responses are mediated by level of threat posed by the hunter, in addition to additional variables which need further exploration.

Cleveland (2012) suggests that due to temporal constraints of human hunters, effects such as landscape of fear may be short lived. Our results support a definitive difference in movement behaviour and response following contacts with deer, what this response is over the mid to long term has not yet been assessed. Gaining a greater understanding of how anti-predator responses impact individual fitness would allow the question of effects on populations to be answered more adequately.

5.2 Habitat

As it has been identified that hunter presence does elicit response in bucks, further investigation included the analysis of habitat related to contacts. Habitat is one of the

most important variables to consider as it is closely linked to life history and behaviour (Simoneaux *et al.*, 2016). It is known that the spatial distribution of vegetation impacts herbivore foraging and herbivores impact abundance and distribution of the vegetation (Tallowin *et al.*, 2005). Additionally, the risk allocation hypothesis, which predicts that movements will decrease in spatial and temporal scenarios with high forage and increase during times with high predation risk (Ferrari *et al.*, 2009). Based on what is known about currently about the strong associations between habitat, behaviour and demography (Riley *et al.*, 2003; Vercauteren and Hygnstrom, 2004), a relationship between anti predator behaviour and habitat is expected.

The first analysis looked at the likelihood of contacts occurring related to habitat variables. Given the hypothesis that deer which move more, are seen more (Roseberry and Klimstra, 1974), in open habitats it was expected that there would be more contacts than in closed canopy or more heavily vegetated habitats. Conversely, it has been suggested that increased movement allows animals to move between resource patches and avoid predation (Sullivan *et al.*, 2018). White-tailed deer thrive in mixed landscapes as they provide both easier cover from predators and abundant food sources, therefore availability of mixed habitat has a strong influence on population demography where available (Riley *et al.*, 2003; Vercauteren and Hygnstrom, 2004). Considering this, I would expect to see increased use of mixed habitats in our results, at least pre-contact.

The analysis found that the intercept habitat (field), road distance and both low and high hunting pressure had significant relationships with the occurrence of a contact compared to their matched pairs. Hunter pressure expectedly had the highest significance in the occurrence of a contact with high hunter pressure showing a p value of 0.005 and low pressure 0.004. It is somewhat surprising, however, that the only habitats that had significant relationships with contact occurrence were field and road distance. Both show a negative relationship with contacts, this is not unexpected for the field habitat, as open habitats allow greater visibility of predators, and therefore to move before they get within the contact threshold of 150m. Wooded habitats still provide adequate cover throughout the duration of this study, with oaks retaining their leaves into January and February (Additionally, as the data was collected in winter, bucks may be more likely to be using

grassy habitats compared to others. Studies of diet in this area of the cross timbers show that grasses are important in the fall and winter diets of deer, woody plants also form an important proportion of seasonal foods during this time, as other foods such as forbs are limited. Thus, woody cover, grassy habitats and food are deeply intertwined this may contribute to the results found in this analysis (Gee *et al.*, 2011). This may be one explanation for some of the findings here relating to habitat which were not significant, whereas previous studies have found that white tailed deer (Henderson *et al.*, 2020) and red deer (Lone *et al.*, 2020) shift habitats to taller/forest cover during hunting season.

Keenan *et al* (2008) found spatial relationships, not only between hunters and deer but between landscape features, such as slope, and land management agents. On public lands it was found that harvest rates, for deer declined farther from roads and on steeper slopes. However, on private lands roads had minimal relationship to harvest rate yet deer on steeper slopes continued to encounter lower harvest rates. Similarly, Lingle (2002) found that elevation affected the movement of white-tailed deer and they moved down and away from slopes in response to coyote predation. Our model, however, showed no significant effect. This may be due to a minimal gradient within our study area which is not very topographically diverse. Further south, close to the river, it might be expected that there would be greater use of slope in predator avoidance behaviour.

The relationship with roads is well established, hunters are more likely to be successful with increasing distance from roads therefore, contacts being negatively correlated with distance to roads is in line with other studies on space use by hunters and ungulates (Rowland *et al.*, 2021). The surprising aspect of this result is that there are limited roads in our study area, most linear features that might be considered roads are two track ATV paths, which were not included in the rasters of road features. Most roads in the study area are around the perimeter of the property, this result suggests that contacts are more likely to occur in core habitat away from the edge areas of the property boundary. This is in keeping with literature that suggests both that there is less disturbance away from roads but also that deer, and other cervid species, are capable of spatial memory (Sutton and O'Dwyer) and therefore would be capable of learning avoidance from features which are heavily used by hunters.

Other habitats did not have a significant relationship. This is surprising given that habitat is one of the greatest predictors of movement and therefore behaviour (Simoneaux *et al.*, 2016). Lebel *et al.* (2012) found that at both local and landscape scales the best predictors of successful deer harvest were a combination of visibility and access. Therefore, habitats with limited visual obstruction from vegetation allowed more observations of deer by hunters. Greater visibility for hunters, however, also would allow greater visibility and threat detection by deer themselves. Therefore, it is possible that while observation is greater, contacts do not increase in open habitats as deer are more vigilant. Other studies have found that deer in hunting season select for more forested cover (Henderson *et al.*, 2020; Little *et al.*, 2014, 2016; Meier, 2021) so there is limited spatial overlap between where deer are most visible to hunters and where deer spend their time in the hunting season. Meier (2021) suggests that deer shift their spatial use to forests and hunters follow them to those habitats due to decreases in visibility of bucks after the beginning of hunting season (Little, 2011). Our results would support this, given the negative relationship between field habitat and likelihood of contacts.

Whilst habitat shows minimal relationships with the likelihood of contacts occurring, it is expected that habitat will mediate the distance at which contacts occur and the flight response of bucks after contacts occur.

The GLMM for post contact flight behaviour did produce one of the only significant associations for habitat of all the models. The landcover post contact showed a very significant relationship with distance travelled at $P = 0.008$. As the habitat was not associated with the likelihood of contacts, this suggests that it's not the habitat the contact occurs in which is important but the availability of habitats to flee to. Given that both grassy habitats and wooded habitats provide important winter food groups for deer in our study area (Gee *et al.*, 2011), the habitat type itself may not be the most important factor in their anti-predator response. Oates *et al.*, (2019) found that when resources are scarce, anti-predator behaviour responses in moose are reduced, instead of shifting their habitats they continue to use their preferred foraging habitat after encounters with moose. Thus, if food resources are poor in our study years, deer may flee to any habitat that is available, instead of selecting for specific habitats. Other recent studies (Dellinger *et al.*, 2019)

suggest that previously assumed relationships between anti predator responses and habitat may not be as clear cut as once thought and may be linked to likelihood of survival of that individual. Their results, however, show that white-tailed deer make use of open habitats so they can detect predators early, and as such, they avoid dense cover in the presence of wolves. These findings contrast that of Meier (2021) that the deer in this study area, use forested habitat more as the hunting season progresses. Maybe this is a clue as to different behavioural responses of deer between mammalian, coursing predators, such as wolves and humans. When you further consider that many human hunters function as lie and wait, ambush predators, it may become advantageous to use cover vs open habitat if individual bucks are unable to see human hunters coming due to use of hides or tree stands. Given all of these considerations, it would suggest that there is more work to be done on study design to fully understand the interactions between deer, style of hunting and habitat selection.

The transition plot shows very similar distributions of habitat type both at contact and 30 minutes after contact. Based on the literature, it would be expected that deer would select for cover habitats post contact with a predator. While the frequencies of each habitat category did not change significantly, there was a 47% change in habitat from time of contact to post contact. Therefore, almost half of deer that experienced contacts did change the habitat type they were in 30 minutes after contact occurred. Field saw the largest change, a decrease of 5% which suggests that whilst deer may not choose one particular cover habitat, they do decrease their use of open, or high risk, habitats following encounters with hunters. Foster *et al.*, (1997) found that vulnerability to harvest displays an inverse relationship with forest % cover. So, a decrease in use of open habitats follows this relationship.

Possible explanations for the lack of clear patterns in habitat use, include spatial memory, distance from cover habitats and risk analysis as per optimal foraging and optimal escape theory. Stankowich and Coss (2007) found that more often than not there was no difference in vegetation height between the origin of a flight and the post flight habitat, although they did find that shorter vegetation at contact resulted in longer flight distances and if there were changes in vegetation height, deer fled to taller vegetation more often

than short. Their results, however, like ours were not significant at the $\alpha = 0.05$ level. This suggests that either habitat is not as important as the body of literature suggests, or there are multiple factors contributing to risk perception and anti-predator responses that cannot be parsed out here. Alternately, as it has been established that deer have already shifted their spatial use of habitat to forest by 1.7-2.5 times as observed by Little (2011), it is possible that this already altered habitat usage is not altered further again by individual contact events. It remains surprising that neither contact distance or flight distance showed any significant relationships with any habitat types other than forest.

Furthermore, Massol *et al.*, (2011) suggests that gaining a better understanding of the relationship between food webs and spatial movement of ungulates is crucial to understanding meta ecologies and resource selection at a landscape scale. So, in addition, the scale at which habitat changes were analysed both temporally, in a very short duration of ~70 minutes and spatially may not allow us to adequately identify changes in habitat use due to predation risk.

When age is incorporated into the model of habitat and post contact flight distance, it is the most significant variable at $P = 0.03$. This is interesting as age, alone, does not show a significant relationship to post contact flight distance. Previous studies, however, suggest that deer are capable of spatial memory, especially regarding food resources. Older deer will have had more prior experiences to inform their anti-predator behaviour and habitat selection post contact with a threat. This may explain the association between age and post contact distance in this model, but not in other models concerning age. Older bucks may be selecting for different cover habitats based on past learned experiences (Sutton and O'Dwyer, 2018).

5.3 Age

Based on the current understanding of learning capabilities in mammals, especially spatial memory (Jakopak *et al.*, 2019; Lewis *et al.*, 2021; Merkel *et al.*, 2019; Ranc *et al.*, 2021; Wolf *et al.*, 2009; Gillingham and Bunnell, 1989), it was expected that there would be a relationship between age and contact behaviour. Prior experience is especially important

to decision making and anti-predator behaviours according to new models on prey escape decisions (Sutton and O'Dwyer, 2018).

When testing the age of bucks against the likelihood of contact although the estimate was negative, which is what would be expected if older bucks were avoiding contacts, the relationship was not significant. This could be for a few reasons. Either bucks really don't learn to avoid hunters as they age or, and more likely, the skewed distribution of ages within our datasets strongly influences the result towards a non-significant p value. There are so few older bucks in the dataset to begin with and no 8.5-year-olds at all in the contact data. Therefore, any relationship that does exist will not be identified due to lack of statistical power. Further analysis may be required with more rigorous testing of data distribution and correction for sample size, to allow adequate analysis of this relationship.

Other research also found no relationship between age and behavioural states, but deer in sample were all similarly aged (Simoneaux *et al.*, 2016). They did, however, find that older deer tend to move less than younger deer. Therefore, if this holds true for our bucks, this may have influenced the likelihood of them having a contact with a hunter in the first place which would explain their absence in the contact dataset. Although our contact vs age did not support this, the model could be adjusted and run again using contact, age, and movement pre contact as a multivariate model to gain a greater understanding of the interdependence of these variables.

It seems there may be a sampling issue when it comes to using age due to the way deer harvests are managed and selection by hunters for attributes associated with different age groups, leading to uneven distributions in age (Strickland *et al.*, 2001; Olson *et al.*, 2010). A meta-analysis of anti-predator movement behaviours across age classes may generate enough samples across age classes for this analysis.

There is also, surprisingly, no relationship between the age of buck and contact distance. This may be due to aforementioned issues with the data. Previous literature has established that experience is influenced by age which therefore affects behaviour as behaviour is dependent on previous experience (Fagan *et al.*, 2013; Nixon *et al.* 1991).

It may be that other factors such as habitat that influence the cost benefit trade off more greatly just have a greater impact than age does on anti-predator behaviours in deer. Alternatively, the relationship between age and anti-predator behaviour is more complex than our statistical analysis could account for. In previous studies, individual variation is often given as a reason for non-significance of relationships, however, newer models that account for individual variation and generate population level estimates are being developed as quantitative methods improve (Sutton and O'Dwyer, 2018).

Finally, the post contact flight distance was tested against age, interestingly unlike contact distance and age which had a positive estimate post contact flight distance has a negative estimate suggesting that with increasing age, the post contact flight distance would be expected to decrease. This is supported by Simoneaux *et al* (2016) which found that older bucks move less overall than younger bucks. Whilst this result is also non-significant, it has the strongest relationship of the three age-based models: likelihood of contact, contact distance and post contact flight distance with a P value of 0.09. Given that age was also statistically significant ($P = 0.03$), in the habitat model (Table 11) it seems this is a true relationship between flight distance and age.

Given what is already known about age of bucks' overall movement, and that bucks in hunting season spend more time in forested habitats, it suggests that older bucks may adapt their habitat use in such a way that large flight distances are not necessary as adequate habitat cover is close by. Additionally, it is possible that older bucks, given their increased capacity for spatial memory, shift their temporal use of habitat to be more nocturnal in open, high risk, habitats and therefore, contacts which occur in daylight hours take place in cover habitats. It has been found that temporal shifts in habitat use occur during hunting season which creates separation between hunters and bucks (Little *et al.*, 2014; Lone *et al.*, 2015). Temporal shifts in activity have also been documented in many other species as an anti-predator response (Higdon *et al.*, 2019).

5.4 Deer ecology and behaviour

Predation, and indirect effects of predation through landscapes of fear, is directly linked to the fitness of an individual and have the potential to impose huge costs on prey species,

that are additive to those found in their evolved life histories (Cherry *et al.*, 2015; Creel and Christianson, 2008). Animals must continuously balance time spent foraging or caring for offspring with self-preservation and defence. The optimal balance is shaped by selection, but human encroachment can up-set this balance and force animals to invest more heavily in defence at the expense of growth and reproduction (Verdolin, 2006; Hebblewhite and Merrill, 2009). The costs of predation are both direct, death where fitness would become 0, and indirect: energy expenditure, missed mating opportunity, displacement from forage etc. (Lind and Cresswell., 2005). Given that many taxa experience lower survival or fitness as a result of increased movement (Biro *et al.*, 2003; Taylor and Knight 2003) these costs potentially reduce the lifetime fitness of individuals and populations, leading to their decline. Whilst spatial and temporal responses anthropogenic harvest have previously been documented (Sullivan *et al.*, 2018), quantifying the intensity of these effects across scales that could be meaningful to wildlife, is still limited (Gutzwiller *et al.*, 2017).

Developing methods that allow the combining of information from multiple sub disciplines to better account for the life histories and fitness costs of individuals responding to threats, across different scales, can give us insight into the true costs of disturbance on wildlife populations.

Our results support previous theories on optimal escape, that responses to predation risk appear to be dependent on several factors and trade-offs. As large carnivores have been extirpated from much of their range, being able to understand the role of human hunters and the effects they exert as predators on deer biology is important to maintaining functioning ecological systems (Schuttler *et al.*, 2016; Flueck, 2000).

There exist substantial differences between human hunting and mammalian predators such as wolves, cougars, and bears. One of the key differences being the temporal limitations of hunting seasons compared to the ever-present risks presented by large carnivores (Manning *et al.*, 2009). New methods, however, are the first step to a more complete understanding of how humans exert costs on game species such as deer.

Developing these models on white-tailed deer, due to their keystone status (Paine, 1969; Waller and Alverson, 1997) creates the potential to influence cascading effects by understanding how human hunting and disturbance of these species impacts their biology and fitness.

Whilst this is only a first step to understanding the trade-offs between risk and benefit in a quantifiable way, this method of identifying dynamic interactions and being able to track subsequent behaviours in individuals, provides a key puzzle piece in creating more accurate models of risk and trade-offs in deer, and other species. Coupled with other methods such as camera traps, to quantify behaviours that cannot be understood from GPS tracking alone, (Olson *et al.*, 2019) and increasingly powerful statistical methods such as those in Sutton and O'Dwyer (2018). Together with interdisciplinary studies of behaviour including behavioural, landscape and movement ecology, along with physiological biology, provide the potential for valuable insights into these behaviours to be gained.

This dataset and modelling did not sufficiently incorporate habitat, a key component of behaviour and fitness potential in deer and other wildlife species. Further developing these methods to more accurately describe habitat use and resource selection functions is critical to their use as a tool for gaining better understanding of deer biology and wildlife more generally. Alternatively, these methods could be used in conjunction with new methods that link the use of habitat to body condition of cervids (Merems *et al.*, 2020). Such interdisciplinary linkages between different fields of ecology will be key to our ability to understand these complex systems and relationships. Purely spatial models cannot capture the full biological nature of these processes, without the addition of methods such as those in Merems *et al.*, (2020).

Trait mediated effects, where predators influence the distribution of prey, have important implications for population biology and can impact whole predator and prey guilds (Muhly *et al.*, 2011) and this can have a knock-on effect on interactions between multiple wildlife species. Therefore, understanding our impacts as a predator on deer has the potential to influence conservation and management at multiple scales in relation to both consumptive and non-consumptive stakeholder groups.

Finally, being able to look at close interactions between individuals in a quantifiable way, has potential implications for our understanding of genetics and inter or intraspecific transmission of pathogens in wildlife populations (Simoneaux *et al.*, 2016). This could be especially beneficial considering the threat that CWD poses to wild cervid populations (Mysterud *et al.*, 2020)

5.5 Hunting as a management tool

Whilst many studies have looked at the direct fitness consequences of hunting, via harvest, less is understood about the indirect costs of hunting and the scale of the impacts (Cromsigt *et al.*, 2013; Munro, 2020) linked to the ecology of fear (Ripple and Beschta, 2003). Given the complex spatial interactions between ungulates, vegetation, abiotic factors, and management (Kramer *et al.*, 2006), there is still a need to gain a more detailed understanding of how hunting impacts both deer populations and achievement of management goals, to ensure longevity sustainable use. Especially as hunting directly, and indirectly, impacts behaviour, life history and demography of species (Creel and Christianson, 2008; Darimont *et al.*, 2009).

By gaining a more accurate method for measuring deer response to predation, and other anthropogenic disturbance, there is increased capacity for the development of holistic models which include both direct and indirect fitness costs to prey species. This is beneficial to wildlife managers, especially as stakeholder groups become more diverse and anthropogenic disturbance to wildlife populations increases (Gaynor *et al.*, 2018). Being able to both identify and accurately quantify escape behaviours provides the opportunity to couple this information with metabolic cost data and habitat resource selection functions to create an accurate picture of the extent to which anthropogenic impacts are affecting individual and population fitness (Christiansen and Lusseau., 2015).

Managing only one cost of fitness on species, through direct harvest, leaves the door open to not adequately account for all impacts on fitness and subsequently mismanage populations. Therefore, using these methods to understand both the direct and indirect effects of hunting, including habitat selection and forage availability, will increase our ability to manage for the population outcomes desired.

Non consumptive effects (NCEs) of predation are becoming more widely recognized but still lack methodologies that can adequately account for all the variables that influence these decisions (Wirsing *et al.*, 2020). Better methods and understanding of risk on spatial behaviour will lead to better management.

5.6 Transferable methods

The negative impact of anthropogenic disturbance and land-use changes on large mammals is becoming increasingly recognised in conservation biology (Torres *et al.*, 2011). Issues concerning anthropogenic impacts from recreation on wildlife populations are complex and there are many different methodologies employed to study these impacts. Marion *et al* (2020) found the most common methods used were: direct observation, telemetry, and camera traps. As previously discussed, this methodology fills a key gap in the use of direct observation by allowing you to accurately measure exactly the movement of the species being observed. This is especially pertinent as outdoor recreation is one of the fastest growing economic sectors in the world (Naidoo and Burton., 2020).

Therefore, being able to quantify the costs of disturbance, and flight behaviour of species' and subsequently the potential to calculate fitness costs, is extremely beneficial to the conservation of species which suffer from recreational anthropogenic disturbance.

Camera traps are a popular method of understanding the impacts of human recreation on wildlife populations. Whilst these are valuable, and non-invasive, tools for measuring disturbance which includes spatial considerations, cameras alone cannot enable us to understand the complexity of disturbance on these wildlife populations. The physiological and behavioural impacts of recreational disturbance are vast (Tablado and Jenni, 2015). Thus, a combination of methods is necessary to gain a clear picture of impacts to these species and the conservation challenges they face.

6 Conclusion

In conclusion the use of GPS telemetry and new methods such as WildlifeDI allows us to better understand and quantify the spatial ecology and behaviour of White-tailed deer in response to predation pressure from human hunters and afford us the opportunity to use these methodologies to answer other pressing conservation questions for mammals in other contexts.

Results show that encounters with human hunters, elicit a behavioural response in White-tailed deer bucks, in the form of elevated step lengths (a proxy for speed) suggesting a flight response, to the perceived threat of humans as predators. It was possible to both identify and quantify the duration of this effect on bucks in the 2008 and 2009 hunting seasons. Additionally, results show that variables associated with contact such as distance from the hunter and the movement of the hunter, influence the response of deer to their presence. This follows the predictions in optimal escape theory on the trade-offs between perceived risks and costs of flight behaviour in response to predators. Allowing us to start filling a knowledge gap on the role of human hunters on fear responses in prey.

The responses shown in the data, are close to those generated by behavioural change of state models, which is a promising sign for the future potential of these models and the capabilities to identify changing behavioural states in wildlife populations using telemetry data.

Habitat attributes did not mediate the flight behaviour of bucks to hunters in the ways that were expected, given the importance of habitat to behaviour and fitness in deer. This suggests the needs for refinement of the methodology to incorporate better habitat selection models or the coupling of this method with other methods, which accurately link habitat use and fitness of individuals in wildlife populations.

Lastly, results showed limited relationships between age of bucks and their response to predation risk from human hunters. This is likely due to constrained statistical power based on sample size but highlights an important consideration when looking at age effects in wildlife populations.

Overall, this research gives us useful insights into both the use of new methodologies to study wildlife populations and the behaviour of wildlife populations in response to a novel predator, including the need for interdisciplinary work to understand the complexities of the behavioural, evolutionary, and spatial response of wildlife to human presence.

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