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The landscape of fear theory proposes that prey should utilize habitat over space and time such that demographic risk is minimized. White-tailed deer *Odocoileus virginianus* respond to temporally and spatially predictable threats posed by humans consistent with the landscape of fear theory. However, few studies examining the response of deer to hunting have accounted for the localized nature of risk. To determine if white-tailed deer are able to recognize and respond to risks posed by hunters relative to specific hunting locations, we equipped 38 female white-tailed deer with GPS collars August–December 2013–2015. Deer were generally found to increase use of feeders, food plots, and vulnerability zones during crepuscular and nocturnal periods as the hunting season progressed. However, deer use of areas around hunting stands decreased during the middle of the day and increased at night in the days immediately following a stand being hunted. We detected no change in use of areas around hunting stands during crepuscular hours in days following when a stand was hunted. Our results suggest that female white-tailed deer are able to recognize and respond to localized risks and do so with a gradient of responses based on localized risk history. However, response was only apparent when analysis accounted for the localized nature of risk, suggesting previous studies may have underestimated the ability of deer to respond to such threats.

All prey species are faced with the challenge of continuously striking a balance between acquiring resources and minimizing risk of predation, with animals that express too much caution risking nutritional deficiencies and reduced fitness, while those that express too little caution risk injury or death (Ferrari et al. 2009, Polivka 2011). However, vulnerability to predators changes according to a variety of factors including spatially, such as how gray wolves *Canis lupus* are most adept at hunting in open meadows (Laundre et al. 2010), or temporally, as in the case of short-eared owls *Asio flammeus* being more efficient hunters on brightly illuminated nights (Clarke 1983). Predictability in predator efficiency, and thus risk of mortality, has given rise to a theory known as the landscape of fear. The landscape of fear theory combines optimal foraging theory, the risk allocation hypothesis, and game theory and suggests that prey should learn from experience and interact with their environment differently over space and time to minimize risk (Laundre et al. 2010). The landscape of

fear theory rests upon three critical assumptions: 1) prey can learn from encounters with predators, 2) predators are not equally efficient across time and habitat types, and 3) prey can identify variations in risk and will modify behaviors in response (Brown et al. 1999, Ferrari et al. 2009, Laundre et al. 2010).

A prime example of the landscape of fear can be seen in the response of white-tailed deer *Odocoileus virginianus* (hereafter deer) to pressure from hunters. The risk deer face from hunters is temporally predictable as hunters can only legally hunt during diurnal hours (Proffitt et al. 2009, Ciuti et al. 2012) and tend to concentrate efforts during crepuscular periods (Proffitt et al. 2009). Hunters are also often spatially predictable as they tend to hunt repeatedly from permanent stands (Cromsigt et al. 2013) and concentrate near roadways (Broseth and Pedersen 2000, Stedman et al. 2004). Deer appear to recognize these risk patterns and react in a manner consistent with the landscape of fear, as previous studies have reported increased use of dense cover and refugia (Autry 1967, Marshall and Whittington 1968, Pilcher and Wampler 1981, Naugle et al. 1997, Kilgo et al. 1998, Kilpatrick et al. 2002, Rhoads et al. 2013), along with increased use of risky areas during non-vulnerable periods such as nocturnal hours (Kilpatrick and Lima 1999). Yet white-tailed deer are not the only cervids that have been

shown to recognize and respond to the predictable nature of hunters, as similar responses have been documented in other species including elk *Cervus elaphus* (Burcham et al. 1999, Millspaugh et al. 2000), mule deer *Odocoileus hemionus* (Kufeld et al. 1988), and roe deer *Capreolus capreolus* (Bonnot et al. 2013).

While deer appear to respond as expected to the landscape of fear when faced with hunting pressure, most previous studies have only examined deer responses to hunting without accounting for the localized nature of the risk these hunters pose. Specifically, early work on this topic reported hunting pressure for the whole landscape in hours per unit area (Autry 1967, Root et al. 1988). While this allowed for coarse insight into response behaviors, it failed to account for the possibility that animals may perceive habitats with fine spatial resolution and integrate that information into behavioral responses. Such incorporation of fine scale spatial data into movements has been seen with numerous species. This is exemplified by the repeated paths used by painted turtles *Chrysemys picta* to reach permanent water bodies following vernal draw down (Roth and Krochmal 2015), the incorporation of high yield flowers into the "trap line" foraging of bumblebees *Bombus terrestris* (Lihoreau et al. 2011), and Brant geese *Branta bernicla* avoiding areas in which they have recently experienced heavy disturbance until food resources in safer areas are depleted (Owens 1977).

Fortunately, some efforts have been made to account for the localized nature of risk when examining the response of white-tailed deer to hunting pressure. For instance, both Karns et al. (2012) and Rhoads et al. (2013) used georeferenced hunting stands to identify areas where deer were at risk during a hunting period, and monitored the use of such areas across time. However, while such an approach met the objectives of their respective studies, neither examined the differences in response to repeated hunting events at these locations. Additionally, both studies defined deer as vulnerable anytime they were in a set distance from any hunting stand. However, habitat differences around stands likely impact actual vulnerability and are likely identifiable to white-tailed deer.

Obtaining information regarding the resolution with which deer perceive risk could dramatically improve our understanding of the spatial reasoning abilities of a critical game species, and examining their spatial and temporal reactions to specific hunting events is the next step in advancing this knowledge. Fortunately, improvements in GPS technology now allow researchers to collect detailed and precise information on animal space use and movement (Gordon 2001, Getz et al. 2007). Pairing GPS data with information on hunter presence would provide a unique opportunity to examine how and when deer respond to the risks posed by a predator. The goal of our study was to determine if female white-tailed deer are able to recognize and respond to the risks posed by hunters relative to specific hunting locations. Our specific research objectives were to 1) characterize space use of female white-tailed deer relative to hunting pressure, 2) determine if female white-tailed deer recognize and respond to specific areas of risk, and 3) determine the temporal influence of risk on the space use of female white-tailed deer. As predicted by the landscape of fear hypothesis,

if deer associate risk with general landscape features (hunting stands, food plots, etc.), then the likelihood of use of that resource type should decrease as the hunting season progresses (Laundre et al. 2010). However, if deer can differentiate risk between specific locations, a landscape wide aversion to a resource type would not be expected, but rather they would avoid particular locations and utilize nearby alternatives.

Study area

Our research was conducted at Brosnan Forest, a 5830-ha tract of lower coastal plain habitat in Dorchester County, South Carolina (33°08′59.1″N, 80°25′72.6″W) and took place on the 2552-ha portion of the property located north of Highway 78. The deer density on this property has been estimated at 20 km^{-2} with a male to female ratio of 1:1.4 (Raglin unpubl.). While the deer hunting season in this portion of South Carolina began annually on 15 August, deer hunting at Brosnan was performed in the mornings and evenings from 15 September – 1 January, with guides transporting hunters to and from fixed locations. Hunting pressure at this site can be described as low (~1.97 h ha^{-1} week^{-1}) since managers purposely rotated use of stands across the property using most stands only a few times per week. Hunting pressure was relatively constant between years. Approximately 93% forested, the study area contained mostly open longleaf pine *Pinus palustris* stands interspersed with mixed hardwoods (Collier et al. 2007). Hardwood drains were found throughout the property with mixed pine-hardwood areas comprised of loblolly *P. taeda*, slash *P. elliottii*, and pond *P. serotina* pine, along with oak *Quercus* spp., sweetgum *Liquidambar styraciflua* and red maple *Acer rubrum*. Bottomland drains included oak, sweetgum, black gum *Nyssa sylvatica* and yellow poplar *Liriodendron tulipifera*. The majority of forest stands were actively managed for wildlife and timber production, and burned on a 2–3 year rotation to maintain an open understory (Collier et al. 2007, Lauerman 2007). Food plots on the study area ranged in size from 0.03–8.5 ha and comprised a total of 119 ha. While a majority of plots were planted annually with a cool season mix of various clovers *Trifolium* spp., grains (oats, *Avena fatua*; wheat, *Triticum aestivum*), chicory *Cichorium intybus* and winter peas *Pisum sativum*, some plots received spring plantings of soybeans *Glycine max*, sorghum *Sorghum bicolor*, or game bird mix containing sorghum *S. bicolor*, buckwheat *Fagopyrum esculentum*, benne *Sesamum indicum* and sunflower *Helianthus* spp. There were also ~55 feeders distributed throughout the study area dispensing shelled corn during the hunting season.

Methods

Capture

During May–August of 2013–2015 we immobilized a total of 43 female white-tailed deer (≥1 year old) via a 2cc transmitter dart (Pneu-dart Inc., Williamsport, Pennsylvania, USA) containing a Xylazine (Lloyd Laboratories, Shenandoah,

Iowa; 100 mg ml^{-1} given at a rate of 2.2 mg kg^{-1}) and Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 100 mg ml^{-1} given at a rate of 4.5 mg kg^{-1}) mixture. Deer were fitted with an ATS G2110D GPS Collar tightened to within approximately two finger widths of the neck, allowing the collar to stay in the proper upright position and improving data accuracy (D'Eon and Delparte 2005). After processing was complete a 3-ml intramuscular injection of Tolazoline (Lloyd Laboratories, Shenandoah, Iowa; 100 mg ml^{-1} given at a rate of 6.6 mg kg^{-1}) was administered to act as a reversal to the Xylazine, and deer were observed until they moved away under their own power. All protocols involving animals were approved by the Auburn University Animal Care and Use Committee (PRN no. 2013-2205).

Data collection and manipulation

Collars were programmed to take GPS fixes at 30-min intervals from 16 August – 1 December, recording position in UTM coordinates, date, time, altitude, fix status, satellites, position dilution of precision (PDOP), horizontal dilution of precision (HDOP), and temperature with each fix. Data were offloaded using ATS WinCollar software, and likely erroneous 3-dimensional fixes with PDOP > 10 or HDOP > 6, and 2-dimensional fixes with HDOP > 3 were removed (D'Eon and Delparte 2005, Lewis et al. 2007).

Following the data acquisition method of Webb et al. (2010), we downloaded the times of sunrise and sunset from the naval observatory website for Summerville, South Carolina (~33 km from the study site). Each fix was then categorized according to the time of day which was represented by three periods: Day-hunting, Day-nonhunting and Night. Day-hunting ranged from one half hour before sunrise until eight in the morning and from three in the afternoon until one half hour after sunset, while Day-nonhunting was from eight in the morning until three in the afternoon. These times were determined based upon when hunters were removed from stands in the morning and delivered to stands in the evening, such that Day-hunting represents times when hunters would be in stands, and Day-nonhunting represents times when stands would generally be unoccupied. Night ranged from one half hour after sunset until one half hour before sunrise. The number of days since the beginning of the hunting season was also recorded for each fix.

We identified three features of the study site (automatic broadcast feeders, food plots and hunting stands) around which we hypothesized deer would change usage patterns relative to their perception of risk. We then recorded the location of each feeder on the study site, and applied a buffer with a radius of 50 m (McCracken et al. 1998, Cederholm 2012), around each via the ArcGIS buffer tool (ver. 10.2; ESRI 2013). Similarly, we documented and digitized the location and shape of each food plot. Finally, we recorded and digitized the location of each hunting stand, and a vulnerability zone around the stand, depicting areas in which deer were vulnerable to hunters (< 200 m from the stand). The vulnerability zone was set by sitting in the stand prior to the beginning of the hunting season and using a laser rangefinder to determine the area in all directions within which a deer would be visible to the hunter. We recorded measurements prior to the beginning of the hunting season to serve

as a conservative estimate, since the loss of foliage during winter would expand the area in which deer were vulnerable. While previous work represented vulnerability zones by setting a uniform buffer around each stand (Karns et al. 2012), we believe that our approach more realistically represented the risk experienced by an animal as variation in vegetation/habitat around a stand would impact the ability of a hunter to detect deer. We then classified each fix as being within or not within a feeder area, a food plot, or a vulnerability zone around a stand. Classifications were made independently and were not mutually exclusive, as the vulnerability zone around a stand could have, but may not have, included a food plot, feeder, or both. We assumed that as the hunting season progressed, decreases in the probability of use of these areas would suggest an aversion due to perceived risk, while an increase would suggest a draw to the available resources (Owens 1977).

Movement rate is widely used and allows for the comparison of results between studies (Root et al. 1988, Kilpatrick and Lima 1999, Karns et al. 2012, Rhoads et al. 2013). To quantify changes in activity throughout the season, we calculated movement rate by finding the average Euclidean distance between consecutive half hour fixes throughout each time period per deer per day (Root et al. 1988, Labisky and Fritzen 1998, Webb et al. 2010, Rhoads et al. 2013). Similar to the censoring method applied by Webb et al. (2010), only daily periods with at least half of the possible consecutive fixes were utilized. The data derived by this metric provide insight into the degree of activity displayed by the animal, and can be interpreted as a measure of response to hunters (Roseberry and Klimstra 1974, Karns et al. 2012). Previous studies have hypothesized that increased movement during periods of hunting pressure result from deer increasing interpatch movement in an effort to avoid hunters, especially in habitats with limited cover (Marshall and Whittington 1968, Root et al. 1988, Rhoads et al. 2013).

Since all hunters were delivered to and picked up from their hunting location by a guide, daily records were maintained regarding which stands were hunted. We determined the nearest stand to each fix via the NEAR tool in ArcGIS (ver. 10.2; ESRI 2013), and recorded the time since hunted, measured in 24-h increments ranging from hunted within the past 24 h through not hunted within the past 169 h. We also recorded the number of hunting events that had previously occurred at the nearest stand for each fix. Changes in the use of the vulnerability zone around a stand following a hunting event demonstrate how deer respond to localized risk, as such changes account for aversion of a single location. Furthermore, the length of time that an animal maintains their aversion toward an area of risk provides insight into the degree of fear the animal has to the experienced risks (Fagan et al. 2013).

Data analysis

We calculated the likelihoods of a deer utilizing a feeder, food plot, and the vulnerability zone around a stand during the Day-hunting, Day-nonhunting and Night periods as a function of the number of days since the beginning of hunting season using logistic regression. We applied a random effect of deer, along with a random effect for the nearest feeder,

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food plot, or vulnerability zone. We predicted probability of use from the logistic regression model for feeders, food plots, and vulnerability zones around stands during each period on days 0, 38, and 77 of the hunting season. Days 0, 38 and 77 represented the beginning, midpoint, and end of hunting, respectively. We calculated movement rate as a function of days since the beginning of hunting season for each time period using linear regression.

We analyzed the likelihood of a deer utilizing the vulnerability zone around a stand as a function of time since hunted, the number of hunting events to date, the number of days since the beginning of the season, and the interaction between time since hunted and number of hunting events to date during Day-hunting, Day-nonhunting and Night via logistic regression. We applied random effects for deer and the nearest vulnerability zone. We predicted the probability of a deer utilizing the vulnerability zone around a stand from the logistic regression model. We conducted all analyses in R (ver. 3.1.3, <www.r-project.org>).

Results

During the course of the study, two deer died prior to the beginning of the study period, two collars malfunctioned, and one collar was unable to be recovered at the time of data analysis, leaving a total of 38 deer. These 38 collars had an average fix success rate, after data censoring, of 87.36% (n = 172 069).

When we examined space use without accounting for the localized nature of risk, number of days since the beginning of hunting was found to significantly impact (p < 0.001) the likelihood of a deer utilizing feeders, food plots, and vulnerability zones around stands during the Day-hunting and Night periods, with likelihood of use increasing each additional day since the beginning of the season (Fig. 1). During the Day-nonhunting period, deer did not significantly alter their usage of feeders (0.786 times less likely, p = 0.203, CI = 0.539–1.147) as the hunting season progressed, but were 0.641 times as likely (p < 0.001, CI = 0.530–0.775) to utilize the vulnerability zone around a stand, and 2.367 times as likely (p < 0.001, CI = 1.787–3.136) to use a food plot on day 77 of hunting as on day 0. On day 0 of the hunting season deer moved an average of 65.3 (SE = 1.5), 40.7 (SE = 1.2), and 80.0 m / 0.5-h (SE = 1.2) during the Day-hunting, Day-nonhunting and Night periods, respectively. Movement rate during the Day-hunting period increased by 0.16 m 0.5-h (p < 0.001, SE = 0.033) with each additional day of hunting. The increase in movement rate equates to an additional 24.64 m h^{-1} during hunting hours on the 77th day of hunting as compared to day 0. Movement rates during the Day-nonhunting (0.04 m/0.5-h; p = 0.143, SE = 0.028) and Night (–0.04 m / 0.5-h, p = 0.148, SE = 0.026) periods did not change with each additional day of hunting.

When we examined the use of vulnerability zones around stands as a function of localized risk, different trends emerged from those seen when localized risk was not taken into account. Deer did not change their usage of vulnerability zones around a stand during the Day-hunting period (Fig. 2A) following additional time since being hunted (1.002
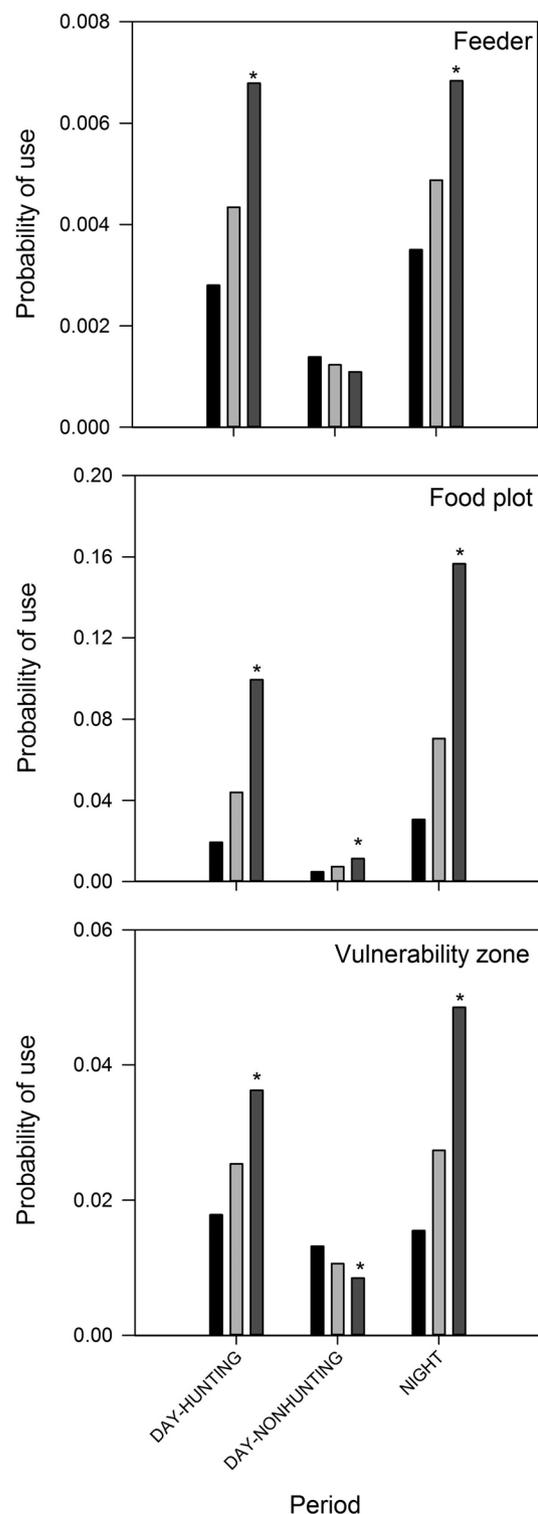

Figure 1. The probability of a female white-tailed deer utilizing a feeder, food plot or the vulnerability zones around hunting stands at Brosnan Forest, SC during any given half hour interval of the Day-hunting, Day-nonhunting and Night periods on days 0 (leftmost bars), 38 (middle bars), and 77 (rightmost bars) of the hunting season, 2013–2015. Asterisks (*) denote models in which the number of days from the start of the hunting season was found to significantly impact use of the resource area (p < 0.05).

times as likely, p = 0.876, CI = 0.971–1.035) or additional hunting events to date (0.976 times as likely, p = 0.373, CI = 0.924–1.031). No significant interaction was found
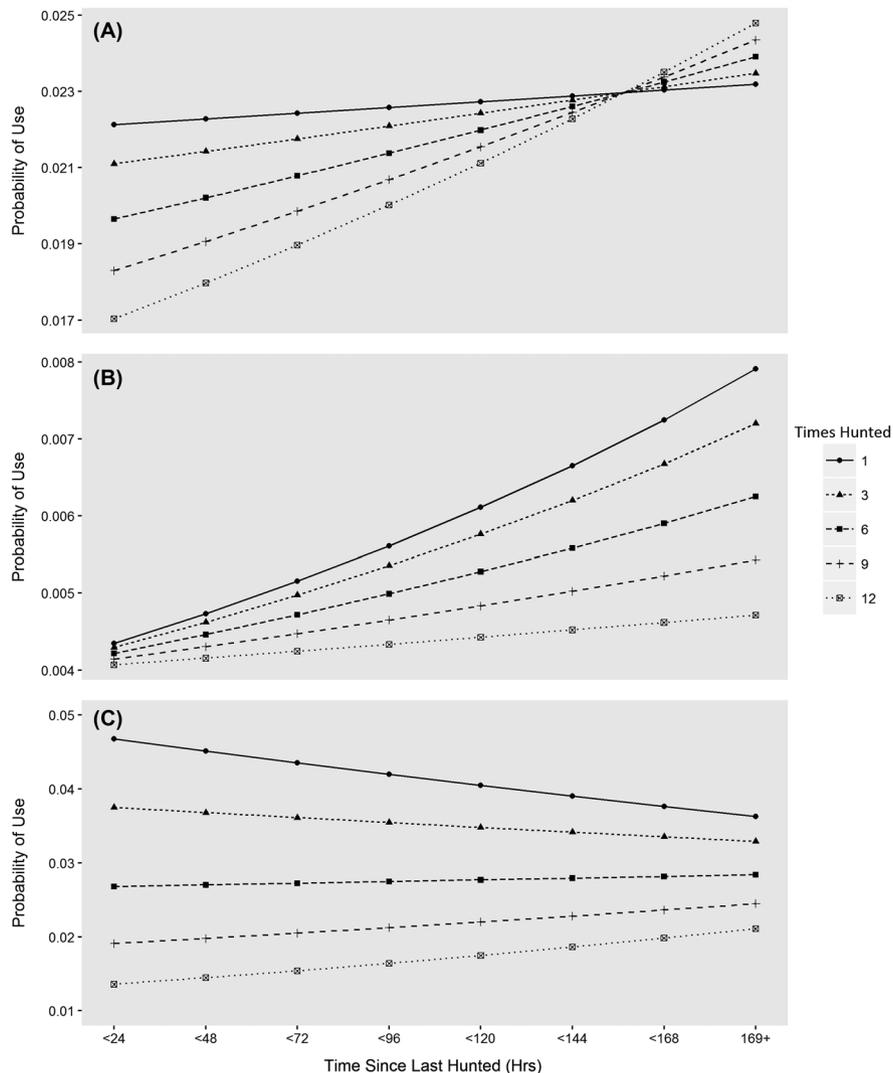
Figure 2. The probability of a female white-tailed deer at Brosnan Forest, SC utilizing the vulnerability zone around a hunting stand during the (A) Day-hunting, (B) Day-nonhunting or (C) Night periods on the 77th day of the hunting season as a function of the time since that stand had been hunted, the number of hunting events at that stand to date, and the interaction between these two variables, 2013–2015.

between these two factors (p = 0.284, SE = 0.004). However, during the Day-nonhunting period deer were 1.010 times as likely (p < 0.001, CI = 1.045–1.149) to utilize the vulnerability zone around a stand following each additional 24-h period after a hunting event, but did not significantly alter usage following additional hunting events (0.994 times as likely, p = 0.880, CI = 0.917–1.077; Fig. 2B). The interaction between time since hunted and number of hunting events was not found to be significant (p = 0.358). During the Night period the likelihood of a deer utilizing the vulnerability zone around a stand was greatest immediately following the first hunting event, and decreased with each subsequent 24-h period after the hunting event (p < 0.001, Fig. 2C). However, this relationship changed following a 4th hunting event, due to a significant interaction (p < 0.001) between time since hunted and number of hunting events, such that the likelihood of use was least immediately following the hunting event and increased with each subsequent 24-h period post hunt.

Discussion

Our data suggest that female white-tailed deer have the capacity to recognize and respond to localized threats posed by hunters through altered behavior and space use. However, this response was not readily apparent when the localized nature of risk was unaccounted for. The increased use of feeders, food plots, and vulnerability zones around stands during the Day-hunting period suggests that the level of hunting pressure was not sufficient to cause deer to avoid these areas ubiquitously across the landscape, which would be the expected response under the landscape of fear hypothesis. The conclusion that hunting pressure was insufficient to impact behavior is supported by a common belief that there is a minimum threshold of hunting pressure which must be met before deer will adjust behaviors to a degree that is observable at the population level (Marshall and Whittington 1968, Root et al. 1988, Karns et al. 2012). An example of this was reported by Karns et al. (2012), who

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concluded that a lack of change in male white-tailed deer space use from pre-hunting to hunting periods, as measured by home range size, core area size, and use of areas surrounding hunting stands, was due to hunting pressure being of insufficient intensity to alter behavior. A similar conclusion was described by Neumann et al. (2009) when they reported a lack of change in moose *Alces alces* behavior during a low pressure hunting period. We believe that increased use of feeders, food plots and vulnerability zones around hunting stands as the season progressed was likely due to deer seeking the food resources these areas provided as native vegetation became less abundant and less palatable during the fall and winter months (Crawford 1982, Johnson et al. 1987). We concurrently observed a general increase in movement rate across the population as the season progressed. As the understory at this site was generally open, such a response would be expected (Marshall and Whittington 1968, Root et al. 1988, Rhoads et al. 2013) as increased movement allowed animals to move between resource patches, thereby avoiding perceived risks while still accessing high value resources. However, some argue that increased movement raises a deer's likelihood of encountering a hunter and thereby further increases risk (Roseberry and Klimstra 1974, Karns et al. 2012).

Hunting season length likely influences how deer respond to risks posed by hunters, due to the tradeoff between nutritional demands and risk avoidance (Lima and Bednekoff 1999, Ferrari et al. 2009). When risk is short lived, any negative effects on fitness due to reduced food access are likely negligible. However, as the duration of risk increases, as would be expected in areas that have hunting seasons that last for several months, the negative effects on fitness due to undernutrition increase and animals should be more likely to engage in risky behavior (Lima and Dill 1989, Ferrari et al. 2009). White-tailed deer have been found to avoid previously preferred habitats such as clear cuts, young pine plantations, and other open habitats during periods of brief hunting pressure (Kilgo et al. 1998). However, in this study, hunting was sustained over several months, suggesting that the nutritional demands experienced by deer throughout the fall could outweigh the risks associated with hunting pressure and drive the behavior we observed when examining space use without accounting for the localized nature of risk (Lima and Bednekoff 1999, Ferrari et al. 2009).

Our data suggest that deer were able to detect hunting pressure and temporally shifted their space use to account for the elevated risk associated with hunting events. An example of this can be seen during the Night period when our study animals responded to the initial hunting events by increasing use of that location during nocturnal hours following the event. We had expected this temporal response to risk, as similar patterns have been documented previously, where deer were found to increase activity during nocturnal hours as a result of hunting pressure (Kilgo et al. 1998, Webb et al. 2010, Karns et al. 2012). Lima and Dill (1989) explained this temporal shift in space use as a strategy by which to reduce the likelihood of encountering risk, as it takes advantage of the temporally predictable nature of hunters. Such a response makes sense when deer recognize risk as temporally restricted, enabling them to minimize risk while remaining

within a known area. Yet, a different response was observed following the fourth time a stand was hunted, where deer displayed the least probability of use the night following the hunting event and increased use thereafter. The response following a fourth hunting event is a fundamentally different response from what was observed during the nights following the first time a stand was hunted, and we interpret this as suggesting that white-tailed deer rely on past experiences to choose between multiple response options after encountering risk. Changes in how deer respond to localized risk as a result of the number of times a location is hunted suggest that white-tailed deer are capable of recognizing localized risks from hunters, storing and modifying this information following additional experiences, and utilizing this cumulative knowledge to minimize risk. However, antipredator behaviors are costly to maintain, and the strength of aversion should decrease over time if risks are no longer encountered (Blumstein 2006, Stankowich and Coss 2007).

We had expected deer to alter their use of hunted locations during their most vulnerable time (Day-hunting). However, the trends observed during this period were not found to be significant, possibly because this period serves as an important feeding window for white-tailed deer (Montgomery 1963, Rouleau et al. 2002). The length of the hunting season at our study area may cause aversion during this window to be unfeasible as it would reduce access to the high value resource areas associated with hunting stands. While the number of times hunted to date lacked a significant effect during both Day-hunting and Day-nonhunting, and time since hunted was not significant during the Day-hunting period, the trends observed do provide an additional indication that deer can perceive the risk posed by hunters and will alter their space use in an effort to minimize risk. It is important to recognize that decreased use of vulnerability zones around occupied hunting locations is different than avoidance due to prior experience. Avoidance of an area the day of hunting is expected (Behrend and Lubeck 1968, Stankowich 2008) and likely indicates detection of the hunter via visual, olfactory, or auditory clues. Conversely, avoiding an area for a length of time greater than the initial exposure demonstrates the ability, for at least some period of time, to create a spatial map of risk and react accordingly (Fagan et al. 2013). Furthermore, the reduction in probability of use with each additional time a stand was hunted suggests that deer recognize a gradient of risk, as opposed to viewing areas as either risky or non-risky (Ferrari et al. 2009). By increasing the strength of the reaction following subsequent hunting events, deer are demonstrating an accumulation of knowledge about the previous risks at specific locations.

The observation of temporary aversion to the vulnerability zone around a hunting stand after that stand had been hunted suggests that low levels of hunting pressure, though previously believed to be non-disruptive (Marshall and Whittington 1968, Root et al. 1988, Karns et al. 2012), do indeed impact deer behavior. However, such impacts are visible only when the localized nature of risk is taken into account. Therefore, previous studies which focused on patterns of space use without accounting for the localized nature

of risk likely failed to identify spatially discrete responses, and thus may have underrepresented risk detection and avoidance abilities of white-tailed deer. For example, Karns et al. (2012) reported that male white-tailed deer utilized areas surrounding permanent deer stands equally during hunting and non-hunting periods for all times of day. These results are similar to our findings that use of high risk areas during hunting hours increased throughout the hunting season. Only by accounting for the temporal nature of risk associated with areas of vulnerability was it possible for us to detect aversive behaviors.

Our findings indicate that white-tailed deer are capable of recognizing and responding to localized risks, suggesting that even limited hunting pressure can impact space use patterns of large cervids. With this approach now established, white-tailed deer can serve as a unique model through which the response of wild cervids to localized risks across gradients of intensity and duration can be examined. White-tailed deer provide a unique opportunity for such research as they are heavily hunted and there is considerable potential to document risk by monitoring hunters. Gaining insight into the role such factors play in the response of white-tailed deer to localized risks will further our understanding of the cognitive processes of large herbivores, as well as provide an indication of what responses can be expected in the face of changing ecosystems. The need for additional research notwithstanding, these results can be taken to suggest that low levels of human disturbance impact animal behaviors (Ditchkoff et al. 2006), and that, instead of attempting to determine if anthropogenic disturbances impact a given species, scientists and policy makers would be better served by looking to understand if the behavioral changes displayed post-disturbance are of biological significance.

References

Autry, D. C. 1967. Movement of white-tailed deer in response to hunting on Crab Orchard National Wildlife Refuge. – PhD thesis, Univ. of Southern Illinois, Carbondale, IL, USA.

Behrend, D. F. and Lubeck, R. A. 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. – J. Wildl. Manage. 32: 615–618.

Blumstein, D. T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. – Ethology 112: 209–217.

Bonnot, N. et al. 2013. Habitat use under predation risk: hunting, roads, and human dwellings influence the spatial behavior of roe deer. – Eur. J. Wildl. Res. 59: 185–193.

Brown, J. S. et al. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. – J. Mammal. 80: 385–399.

Broseth, H. and Pedersen, H. C. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. – J. Appl. Ecol. 37: 182–190.

Burcham, M. et al. 1999. Elk use of private land refuges. – Wildl. Soc. Bull. 27: 833–839.

Cederholm, T. 2012. Use and competition at artificial feeding sites: the roe deer and fallow deer case. First cycle, G2E. – Dept. of Ecology, Grimsö, SLU, Sweden.

Ciuti, S. J. et al. 2012. Effects of humans on behavior of wildlife exceed those of natural predators in the landscape of fear. – PLoS One 7: e50611.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls and deer mice. – Behav. Ecol. Sociobiol. 13: 205–209.

Collier, B. A. et al. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. – J. Wildl. Manage. 71: 277–281.

Crawford, H. S. 1982. Seasonal food selection and digestibility by tame white-tailed deer in central Maine. – J. Wildl. Manage. 46: 974–982.

Cromsigt, J. P. G. M. et al. 2013. Hunting for fear: innovating management of human–wildlife conflicts. – J. Appl. Ecol. 50: 544–549.

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

Ditchkoff, S. S. et al. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. – Urban Ecosyst. 9: 5–12.

ESRI 2013. ArcView GIS. Ver.10.2. – Environmental Systems Research Institute, Redlands, CA.

Fagan, W. F. et al. 2013. Spatial memory and animal movement. – Ecol. Lett. 16: 1316–1329.

Ferrari, M. C. O. et al. 2009. The paradox of risk allocation: a review and prospectus. – Anim. Behav. 78: 579–585.

Getz, W. M. et al. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. – PLoS One 2: e207.

Gordon, I. (ed.) 2001. Proceedings from tracking animals with GIS: an international conference. – Macaulay Land Use Research Center, Aberdeen.

Johnson, M. K. et al. 1987. Effects of cool-season agronomic forages on white-tailed deer. – Wildl. Soc. Bull. 15: 330–339.

Karns, G. R. et al. 2012. Impact of hunting pressure on adult male white-tailed deer behavior. – Proc. Southeastern Assoc. Fish and Wildlife Agencies 66: 120–125.

Kilgo, J. C. et al. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. – Conserv. Biol. 12: 1359–1364.

Kilpatrick, H. J. and Lima, K. K. 1999. Effects of archery hunting on movement and activity of female white-tailed deer in an urban landscape. – Wildl. Soc. Bull. 27: 433–440.

Kilpatrick, H. J. et al. 2002. A shotgun-archery deer hunt in a residential community: evaluation of hunt strategies and effectiveness. – Wildl. Soc. Bull. 30: 478–486.

Kufeld, R. C. et al. 1988. Influence of hunting on movements of female mule deer. – J. Range Manage. 41: 70–72.

Labisky, R. F. and Fritzen, D. E. 1998. Spatial mobiliy of breeding female white-tailed deer in a low-density population. – J. Wildl. Manage. 62: 1329–1334.

Lauerman, S. 2007. Effects of season of fire on red-cockaded woodpecker reproduction and the breeding bird community of a longleaf pine ecosystem. – MS thesis, Clemson Univ., SC, USA.

Laundre, J. W. et al. 2010. The landscape of fear: ecological implications of being afraid. – Open Ecol. J. 3: 1–7.

Lewis, J. S. et al. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. – J. Appl. Ecol. 44: 663–671.

Lihoreau, M. et al. 2011. Tradeoff between travel distance and prioritization of high-reward sites in traplining bumblebees. – Funct. Ecol. 25: 1284–1292.

Lima, S. L. and Dill, L. M. 1989. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

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

Marshall, A. D. and Whittington, R. W. 1968. A telemetric study of deer home ranges and behavior of deer during managed hunts. – Proc. Southeastern Assoc. Fish and Wildlife Agencies 22: 30–46.

McCracken, M. L. et al. 1998. The use of discrete-choice models for evaluating resource selection. – J. Agric. Biol. Environ. Stat. 3: 268–279.

Millspaugh, J. J. et al. 2000. Elk and hunter space-use sharing in South Dakota. – J. Wildl. Manage. 64: 994–1003.

Montgomery, G. G. 1963. Nocturnal movements and activity rhythms of white-tailed deer. – J. Wildl. Manage. 27: 422–427.

Naugle, D. E. et al. 1997. Effects of hunting and loss of escape cover on movements and activity of female white-tailed deer, *Odocoileus virginianus*. – Can. Field Nat. 111: 595–600.

Neumann, W. et al. 2009. The non-impact of hunting on moose Alces alces movement, diurnal activity, and activity range. – Eur. J. Wildl. Res. 55: 255–265.

Owens, N. W. 1977. Responses of wintering brent geese to human disturbance. – Wildfowl 28: 5–14.

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

Polivka, K. M. 2011. Responses to foraging/predation risk tradeoff and individual variability in population-level fitness correlates. – ISRN Ecol. 2011: 1–8.

Proffitt, K. M. et al. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. – J. Wildl. Manage. 73: 345–356.

Rhoads, C. L. et al. 2013. Movements of female exurban white-tailed deer in response to controlled hunts. – Wildl. Soc. Bull. 37: 631–638.

Root, B. G. et al. 1988. Effects of intensive hunting on white-tailed deer movement. – Wildl. Soc. Bull. 16: 145–151.

Roseberry, J. L. and Klimstra, W. B. 1974. Differential vulnerability during a controlled deer harvest. – J. Wildl. Manage. 38: 499–507.

Roth, T. C. and Krochmal, A. R. 2015. The role of age-specific learning and experience for turtles navigating a changing landscape. – Curr. Biol. 25: 333–337.

Rouleau, I. et al. 2002. Contrasting the summer ecology of white-tailed deer inhabiting forested and agricultural landscapes. – Ecoscience 9: 459–469.

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

Stankowich, T. and Coss, R. G. 2007. The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. – Proc. R. Soc. B 274: 175–182.

Stedman, R. D. et al. 2004. Integrating wildlife and human-dimensions research methods to study hunters. – J. Wildl. Manage. 68: 762–773.

Webb, S. L. et al. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. – Int. J. Ecol. 2010: e459610.