

# Impacts of human hunting on spatial behavior of white-tailed deer (*Odocoileus virginianus*)

Sierra A. Marantz, Jed A. Long, Stephen L. Webb, Kenneth L. Gee, Andrew R. Little, and Stephen Demarais

**Abstract:** Predators can influence populations through top-down effects, but most large predators have been extirpated from the range of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)). Hunters have filled this predatory role, but also can indirectly influence prey species. Indirect behavioral responses can include altered resource selection, space use, or movement. Herein, we developed a controlled study that contained both temporal and spatial risk levels to assess how deer behavior changes relative to temporal periods of risk. Total distance travelled and microrange area over 2-day periods were used to determine the general effects of hunting season on deer spatial behavior. Generally, distance travelled, microrange area, and exploratory behavior decreased during the course of the study, with the greatest decrease occurring during the active 16-day hunting period. Despite potential risk and disturbance from hunters, deer maintained site fidelity to previously established ranges and did not expand microrange areas. These data indicate that deer recognize threats from humans on the landscape and adapt behavioral strategies by minimizing movement and exhibiting high residency times in well-established ranges, factors known to influence harvest susceptibility. This information can be used to assess potential impacts from hunting for management purposes, but also to test the adaptive ability of animals to risk.

**Key words:** altered behavior, fidelity, home range, white-tailed deer, *Odocoileus virginianus*, predation risk, GPS tracking.

**Résumé :** Si les prédateurs peuvent influencer des populations par l'entremise d'effets descendants, la plupart des grands prédateurs sont disparus de l'aire de répartition du cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)). Les chasseurs ont joué ce rôle de prédateur, mais peuvent également exercer une influence indirecte sur des espèces de proies. Les réactions comportementales indirectes peuvent comprendre la modification de la sélection des ressources, de l'utilisation de l'espace ou des déplacements. Nous avons conçu une étude contrôlée qui intègre des niveaux de risque tant temporel que spatial afin d'évaluer les changements de comportement des cerfs de Virginie par rapport aux périodes temporelles de risque. La distance totale parcourue et la superficie du microdomaine sur des périodes de deux jours ont été utilisées pour déterminer les effets généraux de la saison de la chasse sur le comportement spatial des cerfs. En général, la distance parcourue, la superficie du microdomaine et le comportement d'exploration ont diminué au fil de l'étude, la plus grande diminution ayant été observée durant la période de chasse active de 16 jours. Malgré le risque potentiel et les perturbations causées par les chasseurs, les cerfs maintenaient leur fidélité aux domaines déjà établis et n'élargissaient pas la superficie de leur microdomaine. Ces données indiquent que les cerfs de Virginie reconnaissent les menaces posées par les humains dans le paysage et adaptent leurs stratégies comportementales en minimisant leurs déplacements et en adoptant de longs temps de résidence dans des domaines bien établis, des facteurs connus pour influencer la probabilité d'être récoltés. Ces renseignements peuvent être utilisés pour évaluer les impacts potentiels de la chasse à des fins de gestion, mais également pour vérifier la capacité d'adaptation au risque des animaux. [Traduit par la Rédaction]

**Mots-clés :** comportement modifié, fidélité, domaine vital, cerf de Virginie, *Odocoileus virginianus*, risque de prédation, suivi par GPS.

## Introduction

Most ecosystems are influenced by human intervention; a primary example of this is the extirpation of large terrestrial predators (Ripple et al. 2014). In this case, human hunters have taken on the dominant predatory role, resulting in an alternative form of predation risk to prey (Frid and Dill 2002; Ripple and Beschta 2004). One area of wildlife movement ecology that is currently understudied is how human presence on the landscape creates

potential risk effects and subsequently influences wildlife movement. In the case of recreational and subsistence hunting, humans represent a unique apex predator (Darimont et al. 2015) and many species (e.g., brown bear (*Ursus arctos* L., 1758): Ordiz et al. 2012; red deer (*Cervus elaphus* L., 1758): Lone et al. 2015) have evolved modified behavior in the presence of hunters (or during hunting seasons). Quantifying wildlife response to actual or perceived human predation risk on the landscape is imperative to understanding hunting

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impacts on wildlife movement behavior, and subsequently, the health of local wildlife populations.

Avoiding predation is a daily contest between predator and prey that can be tied to spatial–temporal processes across the landscape. Although prey have capabilities to directly detect predators, prey often first exhibit indirect methods to minimize detection and encounter rates by predators (Villemain et al. 2015); these effects are known as risk effects, which often are mediated by resource selection or movement behavior. Risk effects are realized when prey must alter their behavior in response to predators (Nelson and Mech 1991; Creel and Christianson 2008). For example, it has been found that male white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) can avoid detection from hunters by changing resource selection and movement patterns (Little et al. 2014). Similarly, western roe deer (*Capreolus capreolus* (L., 1758)) avoid hunters by using less risky habitats (Padié et al. 2015). Instead of altering space use or resource selection, animals may avoid predation simply through changes in mobility or movement tactics.

The aim of this study was to understand how deer change their behavior (movement and space-use metrics) in response to temporal periods of human disturbance and hunting. In a study by Tolon et al. (2009), wild boar (*Sus scrofa* L., 1758) were studied to determine how space-use patterns, such as home ranges, were affected by temporal changes in hunting activity. Based on previous studies and how animals respond to landscape-level threats (e.g., hunting), we hypothesized that prey can respond to risk by shifting space use, or by redistributing the areas used within a home range. The underlying process shaping space use is movement, so we hypothesize that movement patterns will be altered in the presence of hunters. We predicted that male white-tailed deer exhibiting strong site fidelity (Webb et al. 2007, 2010; Hellickson et al. 2008) (i) would not abandon previously used home ranges and would reduce (ii) microrange size, (iii) movement distance, (iv) the use of new microrange areas (Smulders et al. 2012), and (v) exploratory movements. We also predicted that male deer would stop using portions of their microrange as the study progressed (i.e., microrange areas disappear over time, which here we term disappearance (Smulders et al. 2012)). As a result, we expect deer to have to use the spaces within smaller microrange areas more intensively.

## Materials and methods

### Study area

The research was conducted at the Noble Foundation Oswald Road Ranch (NFOR), a 1861 ha research ranch operated by The Samuel Roberts Noble Foundation, Inc., located in south-central, Oklahoma, USA. The region forms part of the Cross Timbers and Prairies ecoregion, which is characterized by a mix of prairie, savannah, and woodland that extends across central Oklahoma, south into Texas, and north into Kansas (Gee et al. 1994; Woods et al. 2005). During hunting season (22 November – 7 December in 2008 and 21 November – 6 December in 2009), mean daily temperatures were 6.7 and 7.2 °C, respectively, and total rainfall was 0.07 cm (2008) and 0.61 cm (2009). At the time of data collection, the ranch did not have any grazing cattle or fire management systems in place. The area is predominantly rural with limited roads. Although all deer were captured on the NFOR, they were not confined to the ranch after being released.

### Capture and GPS tracking

Adult male white-tailed deer were captured using a modified drop-net system that was baited with corn (Gee et al. 1999), sedated using an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg), weighed, and fitted with ear tags and GPS collars (ATS G2000 Remote-Release GPS; Advanced Telemetry Systems, Isanti, Minnesota, USA). As an antagonist to the xylazine, the deer were administered tolazine (0.4 mg/kg), and then released at the capture site. Capture, handling, and marking tech-

niques were approved by the Institutional Animal Care and Use Committee at Mississippi State University (protocol No. 07-034).

All collared deer were adult males, with age estimated using tooth replacement and wear patterns (Severinghaus 1949), from 2.5 to 8.5 years at the time of study. In total, 45 adult male deer were collared (2008:  $n = 25$ ; 2009:  $n = 27$ ), with 7 individuals having data covering both years. However, we restricted analysis to 30 unique individual deer consisting of 37 deer-year combinations (19 in 2008, 18 in 2009); 15 deer were excluded because of illegal or legal harvest prior to the study, mechanical failure of the collar, natural mortality, deer–vehicle collision, and dispersal from the study area (Little et al. 2016). During the study period, GPS collars were programmed to attempt one relocation fix every 8 min. Extreme outliers were removed where the GPS positional dilution of precision (PDOP) reading was  $>10$  (D'Eon and Delparte 2005). The study period was defined as 9 November – 14 December in 2008 and 8 November – 13 December in 2009; a total of 36 days in each year.

### Study design

To evaluate whether adult male white-tailed deer alter their movement and range-use patterns in the presence of hunting across the landscape, we conducted our study during the Oklahoma rifle deer season; hunting at the NFOR site was not allowed during other seasons (i.e., archery or muzzleloader). Across the 36-day period, we developed periods of time that deer could be at risk from human hunters (Table 1). Thus, for the purpose of this study, we use the term “risk” to refer to the presence of hunters within the NFOR site, as human predation via hunting is the dominant form of predation risk to deer in this region. The study consisted of a spatial arrangement of hunted treatments ( $n = 2$ ) and a control treatment (see fig. 1 in Little et al. 2016). A control treatment was used as a safe control without any hunting (2008: 679 ha; 2009: 586 ha) along with a low-density treatment (2008: 586 ha; 2009: 583 ha; resulting in 1 hunter/101 ha) and a high-density treatment (2008: 583 ha; 2009: 679 ha; resulting in 1 hunter/30 ha). Treatment areas were re-randomized during year 2. The two hunted treatments were further divided into hunting compartments to distribute hunters across the landscape at the appropriate density of hunters (Little et al. 2014, 2016). Although the targeted density of hunters was not met each day of the 16-day hunting season, we did, however, maintain the respective ratio of hunters between high- and low-density treatments. Surrounding properties had a variety of hunting effort applied each year, ranging from none to an equivalent of our high-density treatment. However, we could not control or accurately document hunter densities on all surrounding properties. Hunters could not harvest collared deer, but were allowed to harvest 20 females annually, as well as 3 unmarked males in 2008 and 4 unmarked males in 2009.

Over the 36-day study, there were periods where hunters were present and absent (Table 1); we refer to these times as risk-exposure periods. Risk-exposure periods (length (days) of each period are set in parentheses) included pre-season (7 days), scout (2 days), pre-hunt (4 days), hunt (16 days), and post-hunt (7 days). The pre-season period had no hunting activity; the scouting period allowed hunters to enter the study area to learn hunting compartments and locate possible hunting sites; the pre-hunt period was a 4-day period immediately after scouting and in which no human activity was allowed on the study area; the hunting season corresponded to the 16-day Oklahoma rifle season specified each year, with hunters distributed across the property based on density level and compartment assignment (see above); and the post-hunt period immediately followed the rifle season, and again, there was not any hunting activity during this time, although limited human activity occurred on portions of the study area.

Previous analysis demonstrated that deer responded behaviorally (i.e., altered movement behavior) to the presence of hunters where hourly distance travelled by adult males declined across

**Table 1.** Dates for risk-exposure periods of white-tailed deer (*Odocoileus virginianus*) during the 2008 and 2009 study periods.

Risk-exposure period	Year		Hunter presence
	2008	2009	
Pre-season	9–15 Nov.	8–14 Nov.	No
Scout	16–17 Nov.	15–16 Nov.	Yes
Pre-hunt	18–21 Nov.	17–20 Nov.	No
Hunt	22 Nov.–7 Dec.	21 Nov.–6 Dec.	Yes
Post-hunt	8–14 Dec.	7–13 Dec.	No

**Note:** Hunter presence indicates that human hunters either were (Yes) or were not (No) present across the study area. Although we define discrete risk-exposure periods, movement parameters were modeled using generalized linear mixed models to assess relationships and temporal trends over time.

the study period in both density treatments, as well as the safe control treatment (Little et al. 2016). Although there were two density treatments across five discrete temporal risk-exposure periods, we were interested in temporal trends in the data (i.e., modeling the relationship between movement and range use over time) and longer term spatial and temporal processes. We focused on examining the general response of deer behavior to hunters across the landscape by assessing temporal changes in movement and space use over the 36-day study period. Herein, we focus primarily on the temporal dynamics of movement behaviors relative to the presence of risk across the landscape.

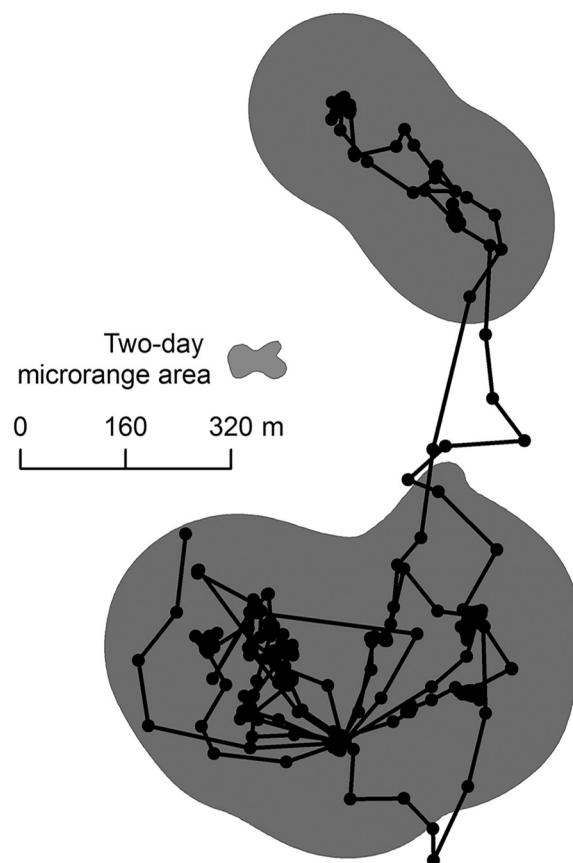
### Movement and ranges

To explore temporal changes in movement behavior, deer GPS data were separated into a series of successive 2-day periods, which overlap day by day (e.g., 8–9 November, 9–10 November, 10–11 November). A 2-day interval was chosen because this was short enough to highlight gradual shifts in deer behavior when using a moving window across overlapping days, but long enough in that it resulted in ~360 GPS locations per interval, which was deemed a suitable number for computing home ranges (sensu Girard et al. 2006). Although the study area was divided into spatial units of varying hunter density, we chose to analyze only the temporal component of the data because of trends found in Little et al. (2016), and the fact that 2-day movement and space-use metrics likely did not occur solely within one treatment area, meaning that deer likely used multiple treatments or areas off of the property. For each 2-day interval, the total movement path length (m) was computed as the sum of the straight-line distances between consecutive points (Fig. 1), which included diurnal and nocturnal relocations.

We also derived a metric to examine the exploratory nature of animal movement (standard deviation of the change in net displacement; SD $\Delta$ ND). First, net displacement (ND) was calculated for each 8-min movement step, where ND is defined as the straight-line (Euclidean) distance from each consecutive fix to the first fix occurring in each 2-day interval. The change in ND ( $\Delta$ ND) was calculated as

$$\Delta\text{ND} = |\text{ND}_{t+1} - \text{ND}_t|$$

where  $\text{ND}_t$  is the present value for net displacement and  $\text{ND}_{t+1}$  is the value for ND at the next telemetry fix. Next, we calculated the standard deviation (SD) of  $\Delta$ ND (SD $\Delta$ ND) for each overlapping 2-day period. We propose that low values of SD $\Delta$ ND will indicate a pattern consistent with spatially and temporally local movement (i.e., high residence times or intensive use of an area), whereas higher values of SD $\Delta$ ND indicate more exploration of the microrange area and lower residency times (see Supplementary Fig. S1).<sup>1</sup>

**Fig. 1.** Example of a 2-day microrange area (and movement path using 8 min relocations) showing an adult male white-tailed deer (*Odocoileus virginianus*) on 11–12 December 2008 in south-central Oklahoma, USA.

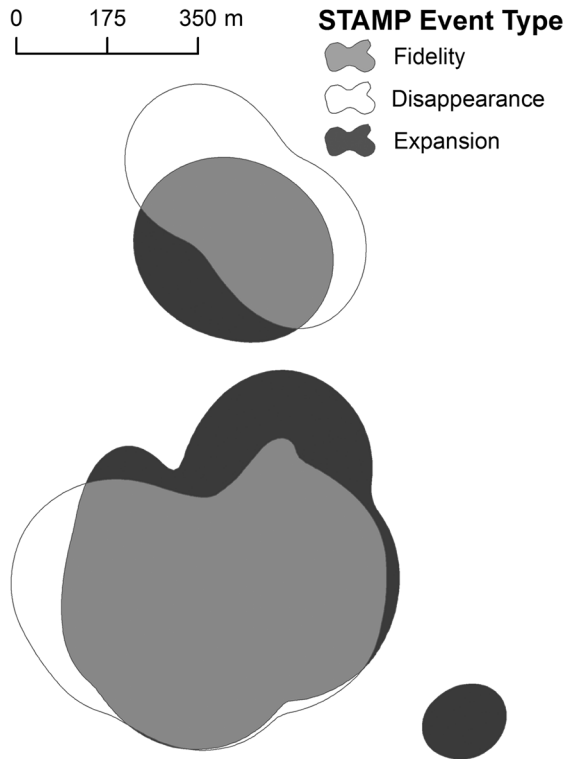
Thus, we consider SD $\Delta$ ND to be a measure of the exploratory nature of movement, especially when interpreted alongside measures of space-use and other movement metrics. We chose SD $\Delta$ ND over the mean  $\Delta$ ND because SD $\Delta$ ND is less correlated with our first movement metric (i.e., movement distance), thus SD $\Delta$ ND is capturing a different characteristic of the data.

Techniques of home-range analysis were then performed to compute microranges, which represent the area used by deer for each 2-day interval. Here again, we used moving windows across 2-day intervals to document temporal changes over the study period. The 95% volume contour from kernel density estimation (KDE) (Worton 1989) was used to delineate each 2-day microrange, using an output grid size of 10 m. Statistical techniques commonly used to estimate the KDE bandwidth can be problematic in the presence of highly autocorrelated tracking data (Hemson et al. 2005). Therefore, we chose to manually determine the bandwidth. We explored three potential bandwidth sizes (i.e., 100, 200, and 300 m) and found that the 200 m bandwidth was an appropriate bandwidth because it was large enough to prevent fragmenting of microranges into multiple areas but small enough to avoid over-smoothing of the microrange (Millsbaugh et al. 2012).

We explored changes, or shifts, in microrange areas using spatial-temporal analysis of moving polygons (STAMP) (Robertson et al. 2007), a GIS-based method for analyzing temporally dynamic polygons. The STAMP approach is useful for assessing topological changes between home ranges (represented as polygons) to quan-

<sup>1</sup>Supplementary Fig. S1 is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0125>.

**Fig. 2.** Example of spatial-temporal analysis of moving polygons (STAMP) events (site fidelity, disappearance, and expansion) for an adult male white-tailed deer (*Odocoileus virginianus*) on 11–12 and 13–14 December 2008 in south-central Oklahoma, USA.



tify spatial-temporal patterns of change (Nelson 2011). The STAMP method adds an additional dimension to the analysis of home-range area by quantifying shifts between two time points (Smulders et al. 2012). Here, we quantify microrange expansion, disappearance, and fidelity. Fidelity represents the home-range area used jointly during both  $T_1$  and  $T_2$ . Disappearance (originally termed contraction in Robertson et al. 2007) represents the area used only in  $T_1$  and not during  $T_2$ . Expansion is the home-range area that developed during  $T_2$ , meaning that it was not present or used during  $T_1$ . We calculated fidelity, disappearance, and expansion areas between microranges for each pair of successive, nonoverlapping 2-day periods (e.g.,  $T_1 = 8–9$  November microrange and  $T_2 = 10–11$  November microrange; Fig. 2). The STAMP area categories were analyzed by dividing each area of disappearance, expansion, and fidelity by the total microrange area for the STAMP period to derive a relative proportion of change.

### Statistical analysis

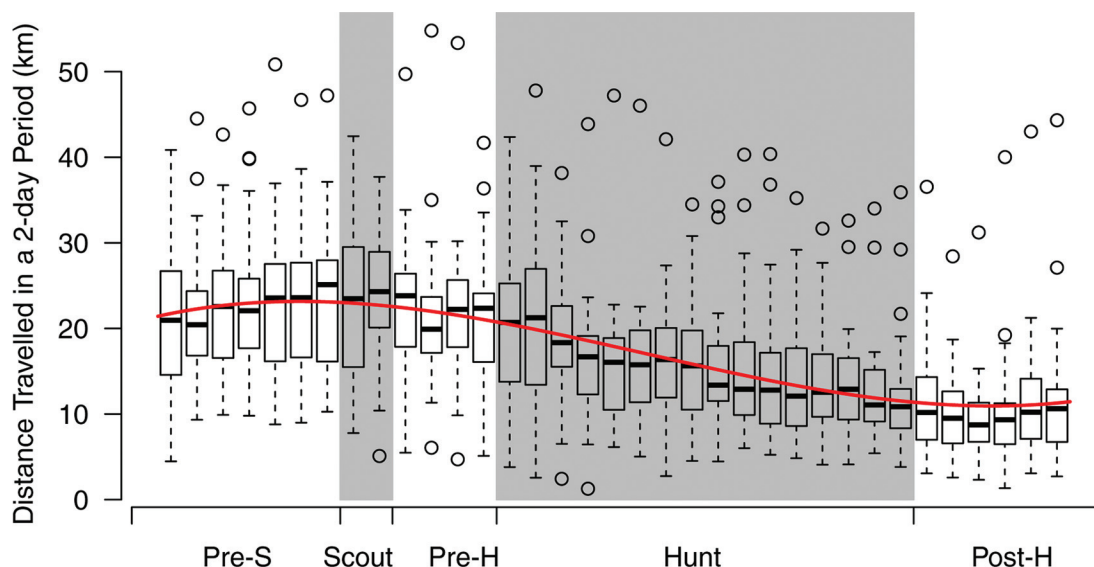
We used generalized linear mixed models (GLMM) using the GLIMMIX procedure in SAS® version 9.3 (SAS Institute Inc., Cary, North Carolina, USA) to describe the relationship between day (independent variable; days 1–36) and each dependent variable (movement distance,  $SD\Delta ND$ , microrange area, disappearance, expansion, and fidelity). Movement distance,  $SD\Delta ND$ , and microrange area were calculated using overlapping 2-day periods to model gradual changes in movement parameters, whereas disappearance, expansion, and fidelity were calculated using nonoverlapping 2-day periods. We modeled linear, quadratic, and third-order polynomial relationships to determine which model best described each dependent variable's relationship with time. We selected the model that best fit the data using Akaike's information criterion (AIC) adjusted for small sample size ( $AIC_c$ ) (Burnham and Anderson 2002). We chose the model with the lowest  $AIC_c$  score as the model best describing the relationship of the data. If the difference in

**Table 2.** Coefficient estimates and statistics of generalized linear mixed models (SAS® version 9.3; SAS Institute Inc., Cary, North Carolina, USA) for 2-day movement distance,  $SD\Delta ND$ , microrange area, disappearance, and expansion over time for adult male white-tailed deer (*Odocoileus virginianus*) in south-central Oklahoma, USA, during the hunting season of 2008 and 2009.

Metric	Intercept ( $\pm SE$ )	Linear ( $\pm SE$ )	Statistic			Statistic			Statistic				
			F	df	P	Quadratic ( $\pm SE$ )	F	df	P	Cubic ( $\pm SE$ )	F	df	P
Movement distance (m)	21 066 (1652.37)	752.29 (155.29)	23.47	1, 1160	$\leq 0.001$	-74.98 (10.08)	55.37	1, 1160	$\leq 0.001$	1.30 (0.19)	49.03	1, 1160	$\leq 0.001$
$SD\Delta ND$	65.937 (5.275)	1.90 (0.507)	14.03	1, 1160	$< 0.001$	-0.19 (0.0329)	33.27	1, 1160	$< 0.001$	0.0033 (0.0006)	29.80	1, 1160	$< 0.001$
Microrange area (m <sup>2</sup> )	1 597 426 (95 903)	71 358 (15 883)	20.18	1, 1192	$\leq 0.001$	-6427.48 (1015.05)	40.10	1, 1192	$\leq 0.001$	107.49 (18.46)	33.92	1, 1192	$\leq 0.001$
Fidelity (%)	0.328 (0.014)	NA	9.91	1, 550	0.002	NA	7.59	1, 550	0.006	NA	NA	NA	NA
Disappearance (%)	0.284 (0.023)	9.02 <sup>-3</sup> (2.87 <sup>-3</sup> )	5.57	1, 550	0.019	-2.3 <sup>-4</sup> (8.2 <sup>-5</sup> )	4.51	1, 550	0.034	NA	NA	NA	NA
Expansion (%)	0.368 (0.02)	-6.49 <sup>-3</sup> (2.75 <sup>-3</sup> )	5.57	1, 550	0.019	1.68 <sup>-4</sup> (7.9 <sup>-5</sup> )	4.51	1, 550	0.034	NA	NA	NA	NA

**Note:** The model for fidelity was not related to time, so the intercept of an intercept-only model is displayed, which is equivalent to mean fidelity.  $SD\Delta ND$  is the standard deviation of the change in net displacement and NA is not applicable.

**Fig. 3.** Box plots and the third-order polynomial relationship (in red) between total 2-day distance travelled by adult male white-tailed deer (*Odocoileus virginianus*) in south-central Oklahoma, USA, and time (see Table 2) that reveals decreasing path length over the 36-day study period (combined for both 2008 and 2009). Periods associated with the presence of hunters are highlighted in grey (see Table 1). Pre-S, pre-season period; Pre-H, pre-hunt period; Post-H, post-hunt period.



AIC<sub>c</sub> between two models was  $\leq 2$ , then we chose the simpler of the two models (i.e., the model with fewest parameters or the lower order model). Although Little et al. (2016) modeled mean hourly movement distance (m) as a linear relationship, data over a longer period of time, such as 2 days, likely would capture more general trends in the response of deer to hunters. Therefore, we used GLMMs and three orders of the relationship to help identify and describe the temporal patterns. With five discrete periods of hunters present or absent, we expected the data to be fit by higher order models to capture the potential risk effects that deer may experience from hunters. Deer identification, year, and deer identification nested within year were modeled as random effects (Littell et al. 2006).

## Results

Total distance traveled (m) over a 2-day period was best described by a third-order polynomial relationship that was related to time (Table 2, Fig. 3), which corresponded with variable periods of hunter presence (Table 1). Over the 7-day pre-season period, movement tended to increase but began to decline during the scout period in which hunters were on the landscape (Fig. 3). Despite a 4-day period without hunters, prior to hunting season, movement continued to decline from the scout period through the hunting season (Fig. 3). Total 2-day movement distance was lowest during the post-hunt period, but began to increase 3 days after the hunting season ended (Fig. 3).

Plotting SD $\Delta$ ND against time (Table 2, Fig. 4), we observed decreasing SD $\Delta$ ND, which would indicate higher residency and less exploratory behavior, resulting in more intense use of micro-ranges by deer during hunting season. SD $\Delta$ ND was best described by a third-order polynomial relationship (Table 2). Examples from this study (see Supplementary Fig. S1)<sup>1</sup> revealed the varying movement patterns associated with different levels of SD $\Delta$ ND, where higher SD $\Delta$ ND was associated with greater mobility and lower SD $\Delta$ ND was associated with encamped behavior (i.e., high residency or intense localized space use).

We observed a similar pattern for microrange area change over the study. Microrange area followed a third-order polynomial relationship (Table 2, Fig. 5), where area increased during the pre-season period followed by a slow decrease in area used from the scout to the pre-hunt periods (Fig. 5). The greatest decline in area

occurred during the hunting season, culminating in the smallest microrange area during the post-hunt period before starting to increase in area (Fig. 5).

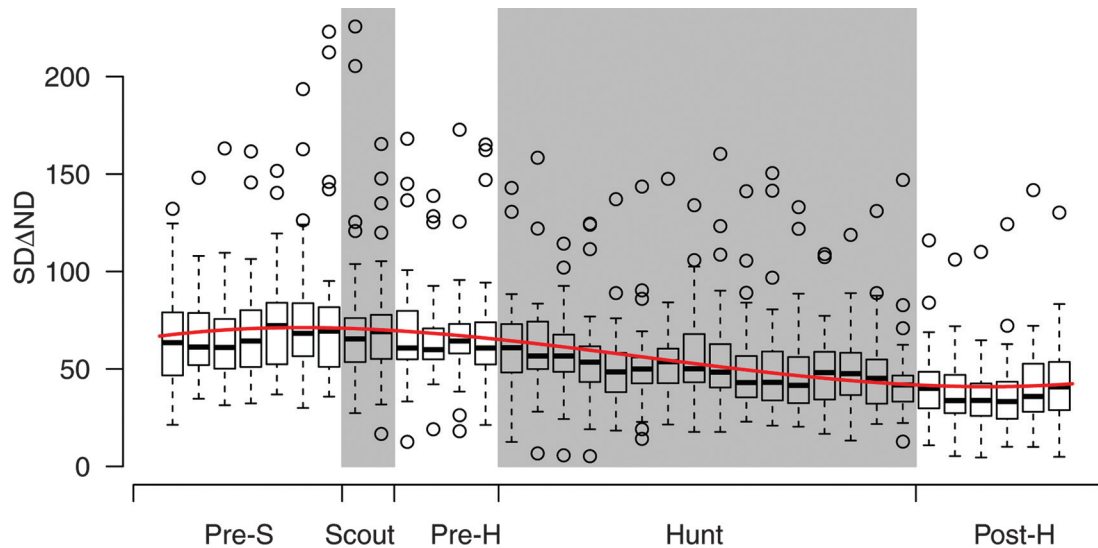
Fidelity did not change over time and averaged  $0.33 (\pm 0.01 \text{ SE})$ ; Fig. 6a). However, we did observe greater disappearance of previously used areas during the hunting season, which was best characterized by a quadratic relationship (Table 2); disappearance was less before and after the hunting season (Fig. 6b). Range expansion, or use of new areas during  $T_2$  compared with  $T_1$ , also followed a quadratic relationship (Table 2), but showed an inverse relationship compared with range disappearance where expansion was least during the hunting season and greater before and after the hunting season (Fig. 6c). The findings of decreased microrange areas over time, as well as decreased range expansion and increased disappearance, provide evidence that deer concentrated activities within a smaller area, relative to their total range, during times of perceived risk on the landscape (as indicated by increased disappearance) without expanding the area used greatly.

## Discussion

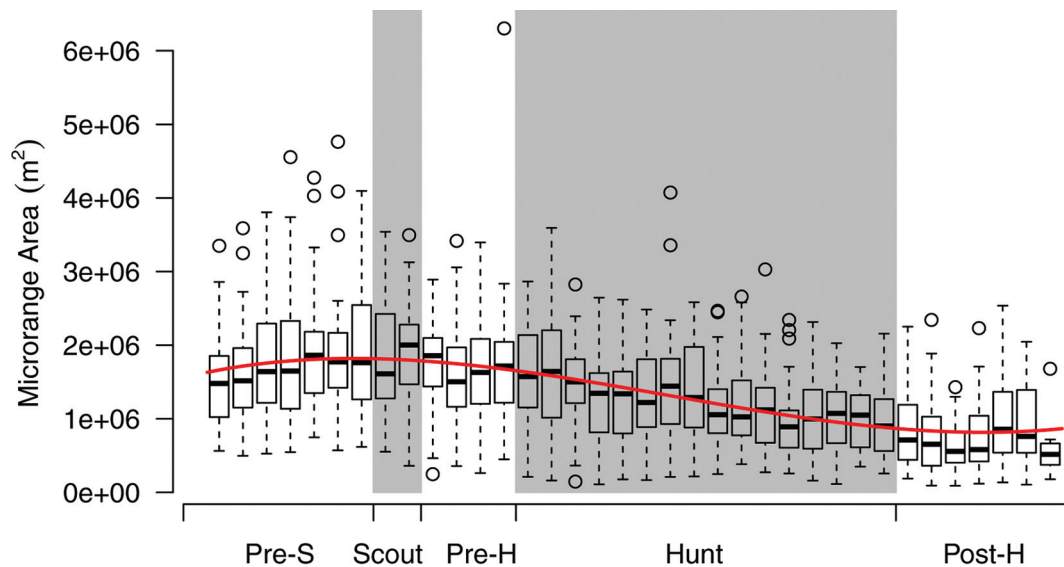
Hunters caused deer to alter movement and space-use behavior. A previously conducted meta-analysis showed that ungulates in hunted populations had greater flight responses than ungulates in nonhunted populations (Stankowich 2008). Our results suggest that in a strictly hunted population, deer mediated the potential risk posed by the presence of hunters by altering movement; furthermore, the response of deer to hunter presence occurred rapidly once deer detected humans on the landscape (i.e., during the scout period; see also Lone et al. 2015). We also found that deer exhibited a stronger movement response (i.e., declining movement and space use) during the hunt period.

Few studies, if any, have the ability to collect enough GPS locations over short temporal windows for estimating home ranges. Using 8-min relocations, we were able to estimate 2-day movement and space-use metrics using up to 360 GPS locations. Modeling movement and space use at finer temporal scales may be required to detect when, and to what magnitude, predation risk affects behavior. For example, Creel and Winnie (2005) observed that herd size of elk (*Cervus elaphus* L., 1758) increased only on days when wolves were present. In the present study, we found that once hunters first appeared on the landscape (i.e., scout period),

**Fig. 4.** Box plots and modelled relationship of the standard deviation of net displacement (SD $\Delta$ ND) metric over time. The SD $\Delta$ ND was best described by a third-order polynomial relationship (in red; see Table 2). All data were for adult male white-tailed deer (*Odocoileus virginianus*) in south-central Oklahoma, USA, over the 36-day study period (combined for both 2008 and 2009). Periods associated with the presence of hunters are highlighted in grey (see Table 1). Pre-S, pre-season period; Pre-H, pre-hunt period; Post-H, post-hunt period.



**Fig. 5.** Box plots and the third-order polynomial relationship (in red) between 2-day microrange area used by adult male white-tailed deer (*Odocoileus virginianus*) in south-central Oklahoma, USA, and time (see Table 2) that reveals decreasing microrange area over the 36-day study period (combined for both 2008 and 2009). Periods associated with the presence of hunters are highlighted in grey (see Table 1). Pre-S, pre-season period; Pre-H, pre-hunt period; Post-H, post-hunt period.

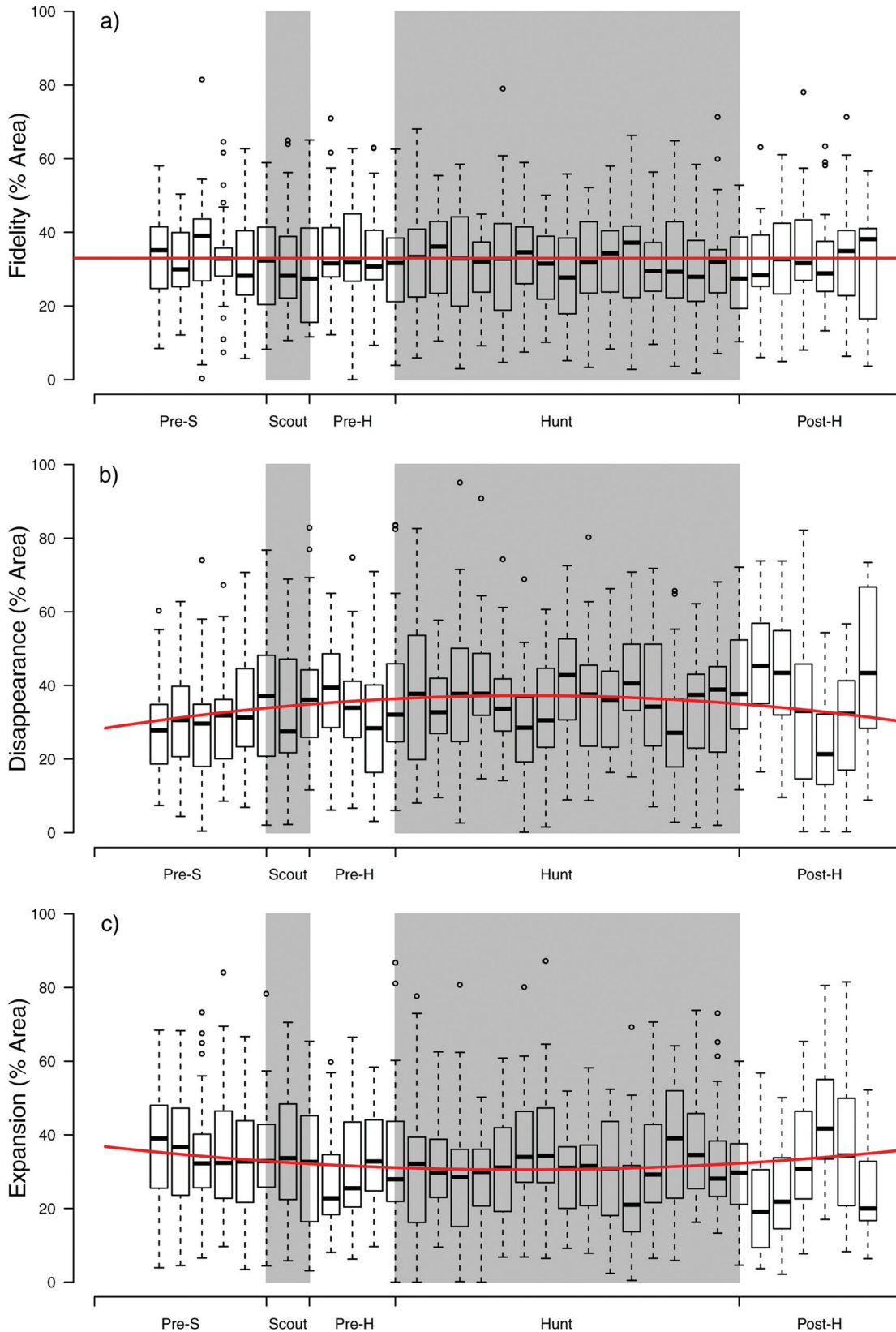


deer exhibited a behavioral change that resulted in declining movement and space-use patterns, even during a period without hunters (i.e., pre-hunt period) and with minimal increases in movement and space use after hunters were entirely removed from the landscape (i.e., post-season period).

Moving prey often are detected more by predators (Lima and Dill 1990). Therefore, we predicted that deer would reduce movements to avoid detection by hunters during the hunting season (Little et al. 2014); this prediction was supported by these findings in that total distance travelled over 2 days declined at the greatest rate during the hunting season. Most often, flight responses do not last over long periods of time (Frid and Dill 2002). We observed a pattern that is similar to this prediction in that deer generally adjusted their behavior in the presence of hunters, likely to avoid detection. If flight responses (e.g., extremely long movement dis-

stances) were more predominant, then we would expect the microrange area to increase because deer likely would have used additional area. It is important to note that we calculated 95% microranges for each 2-day period, so some flight responses may not have been captured by the microrange, but over time, flight responses would have been detected especially if deer had to use temporary refuges after the flight response. Because many flight responses were not readily observed in the space-use analysis, this also lends support to their relatively rare occurrence, suggesting that areas of refuge within previously used ranges may have offered enough protection to avoid detection and having to flee in response to a threat. These results are similar to those noted by Karns et al. (2012), who found that under conditions of limited hunting pressure, deer return to their home ranges after events of disturbance. Although the post-hunt period indicates stabilization in

**Fig. 6.** Box plots showing changes over time for each STAMP event type: (a) fidelity, (b) disappearance, and (c) expansion. Quadratic relationships (in red; see Table 2) show the relationship between disappearance and expansion of microrange area for adult male white-tailed deer (*Odocoileus virginianus*) in south-central Oklahoma, USA, over the 36-day study period (combined for both 2008 and 2009); site fidelity did not change over time and averaged 33%. Periods associated with the presence of hunters are highlighted in grey (see Table 1). Pre-S, pre-season period; Pre-H, pre-hunt period; Post-H, post-hunt period.



2-day distance travelled and microrange area, this may continue to change over longer post-hunt periods as the deer respond to a lack of hunters on the landscape. Although this study does not investigate changes in habitat type (e.g., from using more open to more wooded areas during hunt), deer have been found to alter their movements in favor of more concealed areas to avoid hunting activities (Kamei et al. 2010; Little et al. 2014).

Movement is the underlying mechanism shaping space use and dynamics, so we also predicted that size of the microrange area would decrease during the hunting season whereby deer would be using smaller areas more intensively. Again, our prediction of decreasing size of the microrange area was supported. Reducing extent of space may be a strategy to minimize human contacts or predation risk (Webb et al. 2011b). In elk, females used smaller areas more intensively in the presence of human activity (Webb et al. 2011a). However, in male white-tailed deer, home ranges and core areas may not be affected by hunting in that sizes of deer ranges were found to be similar between pre-hunt and hunt periods in a study by Karns et al. (2012). Therefore, reduced movements in more confined areas potentially decreases the chance of being exposed to risk effects.

Shifting ranges may be a result of behavior in which deer react to risk effects in the area to avoid interaction with, or concealing themselves from, hunters. Male deer exhibited fidelity to previously established microranges, which averaged 33% over the course of the study. We predicted increased site fidelity because deer become intimately familiar with their ranges, which may confer survival advantages by avoiding detection from hunters or eluding predators. However, we found that site fidelity did not increase, but remained constant over time, with some changes in space use resulting from shifts of use within larger, previously used areas. It follows then that remaining within a familiar range will be more efficient at reducing risk than moving to novel areas (Padié et al. 2015). Elk showed strong site fidelity in response to increasing human development, but did redistribute their home ranges to areas with less development (Webb et al. 2011b). Similar to elk, adult male white-tailed deer in this study appeared to remain loyal to previously established areas but would adjust space-use patterns over the 2-day windows, likely to minimize risk from hunters on the landscape. If deer are to take advantage of familiar surroundings through strong site fidelity, then they should not expand range-use size or move into novel environments. Also, deer may have greater advantages when using smaller ranges, so it makes sense to reduce the amount of area used in the presence of predation risk. These two behaviors were supported in that range expansion was minimal during hunting season, whereas disappearance of previously used areas was greatest during hunting season. Similarly, roe deer did not shift the location of their home ranges once the high-risk period began (Padié et al. 2015).

Deer use within a range also may be affected by predation risk. When faced by predation risk, deer may exhibit short-term flight responses, but only when necessary, so deer should generally show less displacement or exploration (i.e., greater residency) over longer periods of time, which was indicated by SDAND. Therefore, a general avoidance strategy would be to adopt high residency and confine movements to focal areas within known areas (microranges). SDAND suggests that residency times during hunting season were greater (e.g., localized or concentrated use likely to avoid detection or hunters), resulting in more intensive use of smaller microranges. High residency times equating to localized use of smaller spatial extents may be a hiding strategy to stay concealed from potential predators.

It also is important to note that the breeding season for white-tailed deer occurs in mid- to late November, coinciding with the hunting season (Nixon et al. 1991). Male deer in this study were of breeding age and thus were expected to exhibit typical rut behavior, which has been reported to include expanding range size (Kammermeyer and Marchinton 1976; Nelson and Mech 1981;

Nixon et al. 1991) or movements (Webb et al. 2010; Foley et al. 2015). However, any increases in movement that deer might exhibit during the rut appear to be eclipsed by predation risk from hunters in this study. We note that these data included diurnal and nocturnal GPS relocations, which could have dampened the effect from hunting because deer likely perceived that hunters were not present on the landscape at night and exhibited greater movement patterns. Despite the fact that movement could be greater at night, which has been noted (Little et al. 2016), we still observed strong trends to reduce movement as the study progressed. Of course, other factors influence movement and space-use patterns; for example, another primary driver of movement is forage availability. We would further hypothesize that both rut and forage availability, which often is less at this time of year, would result in greater movements. However, we still documented decreasing movement and space use over the study period, providing evidence that hunters are a driving force shaping deer space-use behavior at this time of the year.

Characterizing the behavioral response of deer during hunting season required high-resolution and frequent GPS data coupled with modern analytical tools (e.g., STAMP) and sophisticated statistical analyses (e.g., GLMM). We performed both path-based analysis (i.e., movement distance, SDAND) and polygon-based analysis (i.e., STAMP) to understand changes in movement behavior over time. Our analysis used a moving temporal window approach, which can be criticized for introducing implicit temporal autocorrelation, but can be modeled statistically; it also has the advantage of further generalizing the data to identify underlying patterns and trends. Using generalized linear mixed models, we leveraged robust parametric approaches to model functional relationships of interest that characterized and corresponded to the presence of hunters. Box plots further augmented the level of information presented in these models by showing finer scale nuances in the data. Other approaches can be used to elicit similar interpretations such as general additive (mixed) models (Ciuti et al. 2012), but here we chose GLMM due to their parametric form, their statistical robustness, and their insensitivity to sampling error. The best-fit model equations capture the nature of the dynamic temporal response of deer to hunting season and will serve as the basis for future quantitative testing.

The overall response of male deer to human hunters showed trends that supported predictions of how deer would respond in the presence of perceived risk from hunters. It appears that male deer respond spatially to temporal risk from hunters in general (mean response and trends), but also appear to respond in situation-specific manners (large variation around the mean). In elk, modified behavior and resource selection have been found to reduce the probability of mortality (Webb et al. 2011c; Dzialak et al. 2011). It appears that adult male deer are able to adopt strategies that lend themselves to avoiding detection by hunters (Little et al. 2016), so these strategies likely could increase fitness through increased survival when deer are not at risk of harvest. However, the avoidance of risk through altered movement is likely further mediated by changing resource-selection patterns, which was indicated by earlier analyses (Little 2011).

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