Hunting intensity alters movement behaviour of white-tailed deer

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Abstract

Recreational hunters have largely replaced natural predators of white-tailed deer (*Odocoileus virginianus*) across much of North America; thereby, providing the greatest form of risk (both direct and indirect) to survival. On a 1861-ha property in Oklahoma, USA, we evaluated how controlled hunting influenced movement behaviour (using movement rate [m/h] and relative displacement index [%]) of 37 adult ($\geq$2.5 years) male deer at three risk treatment levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha), two temporal periods of risk (i.e., diurnal [06:00–18:00] and nocturnal [18:00–06:00]), and across time (36 days); time was modelled as a continuous variable that covered five risk exposure periods (risk present or absent in brackets; i.e., pre-season [absent], scout [present], pre-hunt [absent], hunt [present], and post-hunt [absent]). Movement rate (m/h) decreased over time for all risk treatment levels and temporal period of risks; however, the magnitude (i.e., slope) of decrease varied across treatments. The magnitude of decrease in movement rate was similar for control and low risk treatments during diurnal and nocturnal periods, but was different between low and high risk, and high risk and control treatments. Relative displacement (%) of deer was greatest at the start of the study, decreasing during the study finally resulting in displacement values being three times less after hunting season. Deer responded to the presence of hunters on the landscape by adapting movement strategies both spatially and temporally to avoid potential contact with hunters. During the study, deer reduced movements and used smaller areas more intensively, as indicated by the relative displacement index. Reducing movement or space use may lead to lower detection of deer by hunters, thus increasing the probability of survival through reduced harvest. Understanding deer behavioural responses to hunters (and at different levels of risk) could be used to facilitate or reduce harvest based on population management objectives.

Zusammenfassung

Freizeitjäger haben die natürlichen Räuber der Weißwedelhirsche (*Odocoileus virginianus*) in weiten Teilen Nordamerikas ersetzt und sind der wichtigste Risikofaktor (sowohl direkt als auch indirekt) für deren Überleben. Auf einem 1861-ha-Anwesen in Oklahoma (USA) untersuchten wir, wie kontrollierte Bejagung das Bewegungsverhalten (Bewegungsrate = m/h) und den

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relativen Ortsveränderungsindex (%) von 37 adulten (Alter ≥2.5 Jahre) Hirschen beeinflusste. Wir betrachteten drei Risikostufen (Kontrolle = kein Risiko, geringes Risiko = 1 Jäger/101 ha und hohes Risiko = 1 Jäger/30 ha), zwei Tageszeiten (tagsüber und nachts) sowie den Zeitverlauf (36 Tage). Die Zeit wurde als eine kontinuierliche Variable modelliert, die fünf Risiko-Perioden abdeckte: Vorsaison (kein Risiko), Erkundungsphase (Risiko), Ruhe vor der Jagd (kein Risiko), Jagdzeit (Risiko) und Nach-Jagd-Phase (kein Risiko). Die Bewegungsrate nahm über die Zeit bei allen Risikostufen ab, aber das Ausmaß der Abnahme variierte zwischen den Behandlungen. Die Abnahme der Bewegungsrate war ähnlich für die Kontrolle und bei geringem Risiko während der Nacht und tagsüber, aber es gab Unterschiede zwischen der Hoch-Risiko-Behandlung und den beiden anderen Behandlungen. Die relative Ortsveränderung der Hirsche war am Anfang der Untersuchung am größten und nahm mit der Zeit bis auf ein Drittel des Ausgangswertes in der Nachsaison ab. Die Hirsche reagierten auf die Anwesenheit von Jägern im Gelände, indem sie ihre Bewegungen räumlich und zeitlich anpassten, um möglichen Kontakt mit Jägern zu vermeiden. Sie reduzierten ihre Bewegungen und nutzten kleinere Gebiete intensiver. Dies könnte dazu führen, dass die Hirsche seltener von Jägern aufgespürt werden, wodurch die Überlebenswahrscheinlichkeit durch geringeren Abschuss steigt. Die Kenntnis der Reaktionen der Hirsche auf Jäger (und bei unterschiedlichen Risikostufen) könnte dafür genutzt werden, entsprechend der Ziele des Populationsmanagements Abschüsse zu erleichtern oder zu reduzieren.

Introduction

Presently, recreational hunters are a prominent force at shaping population dynamics of large ungulates across much of North America, and for many cervids, hunters may be the greatest form of risk (both direct and indirect) to survival. Because of the direct harvest of game animals by hunters, as well as disturbance from humans, Frid and Dill (2002) suggested that prey approached by humans likely respond similarly to those approached by other predators, thus there are perceived predation risk effects associated with humans. Animal response to human predation risk varies greatly depending on the type of risk, environment and temporal scale (Dasmann & Taber 1956; Van Etten, Switzenberg, & Eberhardt 1956; Kammermeyer & Marchinton 1975; Kilgo, Labisky, & Fritzen 1998; Karns, Lancia, DePerno, & Conner 2012). Hunting probably has the greatest potential to create risk effects, which can cause game animals to alter spatial distributions and behaviour to reduce the potential threat of harvest or disturbance (Cromsigt et al. 2013). Not only can humans directly take wildlife (i.e., harvest), but the risk effects potentially can have fitness consequences whereby survival and reproduction suffer when animals make trade-offs between risk avoidance and energy acquisition (Gill & Sutherland 2000). Today, overabundant populations of game animals such as white-tailed deer (*Odocoileus virginianus*) can cause human–wildlife conflicts that cannot be overcome by harvest alone. Because of the potential direct and indirect effects of human predation risk, managing game animals by altering their spatial distribution and behaviour may be an alternative to reducing population numbers (Cromsigt et al. 2013).

Human predation risk is likely to elicit greater responses from animals as perceived risk of predation increases (Frid & Dill 2002). Animal response to predation risk is commonly evaluated by examining movement behaviour (Miller, Garner, & Mench 2006; Stankowich 2008). For example, movement rate of elk (*Cervus elaphus*), when exposed to human predation risk, increased during intensive hunting seasons in Montana (Cleveland, Hebblewhite, Thompson, & Henderson 2012). Similarly, in white-tailed deer, human hunting activity may influence movement or space use patterns (Autry 1967; Sparrowe & Springer 1970; Pilcher & Wampler 1981; Root, Fritzell, & Giessman 1988). However, it is unknown how the redistribution of animals after disturbance will affect other fitness producing activities (Gill, Sutherland, & Watkinson 1996). Changing behaviour or distribution patterns, most often through changes in movement, can either impede the risk of predation, or increase the vulnerability of the animal to predation when the predation event is dependent on the change in behaviour (Little et al. 2014). For white-tailed deer, understanding hunt-related movements by deer is important because they can directly influence harvest recommendations and management success (Rhoads, Bowman, & Eyler 2013). For example, deer are more vulnerable to harvest as they move more as a result of hunter presence and associated risk depending on the timing of the hunting season in relation to breeding season (Little et al. 2014), thereby facilitating harvest through increased vulnerability of the prey when exposed to risky situations. Conversely, if deer move less in the presence of human predation risk, then harvest requirements may not be met because too few deer are observed and harvested (Little et al. 2014).

To address the effects of hunters on wildlife behaviour, we focused our study on white-tailed deer, one of the most widely hunted big-game animals in North America (Halls 1973). Hunters are filling the predatory role once held by natural predators for the purposes of managing white-tailed deer in much of North America. However, a paucity of information

exists on whether hunters cause deer to alter movement behaviour to avoid risk of predation, which ultimately could influence the efficacy of meeting management objectives (e.g., harvest recommendations, population size reduction, etc.). Therefore, our research evaluated behavioural responses (i.e., changes in movement rate and displacement) of white-tailed deer to human predation risk. This study employed a designed experimental approach whereby human predation risk (hunters) was varied, but controlled, at three risk treatment levels (i.e., control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha). We also incorporated two temporal periods of risk and five risk exposure periods into the analysis. Temporal periods of risk included diurnal hours (06:00–18:00) when hunters (i.e., the predator) were present and nocturnal hours (18:00–06:00) when hunters were absent. Last, we assessed a time trend model

on movement metrics over the course of the 36-day study period. Our objectives were to determine effects of: (1) risk treatment level, (2) temporal period risk, and (3) time (continuous variable; $n = 36$ days) on white-tailed deer movement behaviour (i.e., movement rate and relative displacement).

Materials and methods

Study area

We conducted this study on The Samuel Roberts Noble Foundation's Oswalt Ranch (NFOR) in Love County, Oklahoma (Fig. 1). The NFOR is a 1861-ha ranch located in the Cross Timbers and Prairies eco-region characterized by a mixture of wooded areas, bottomlands, uplands, and
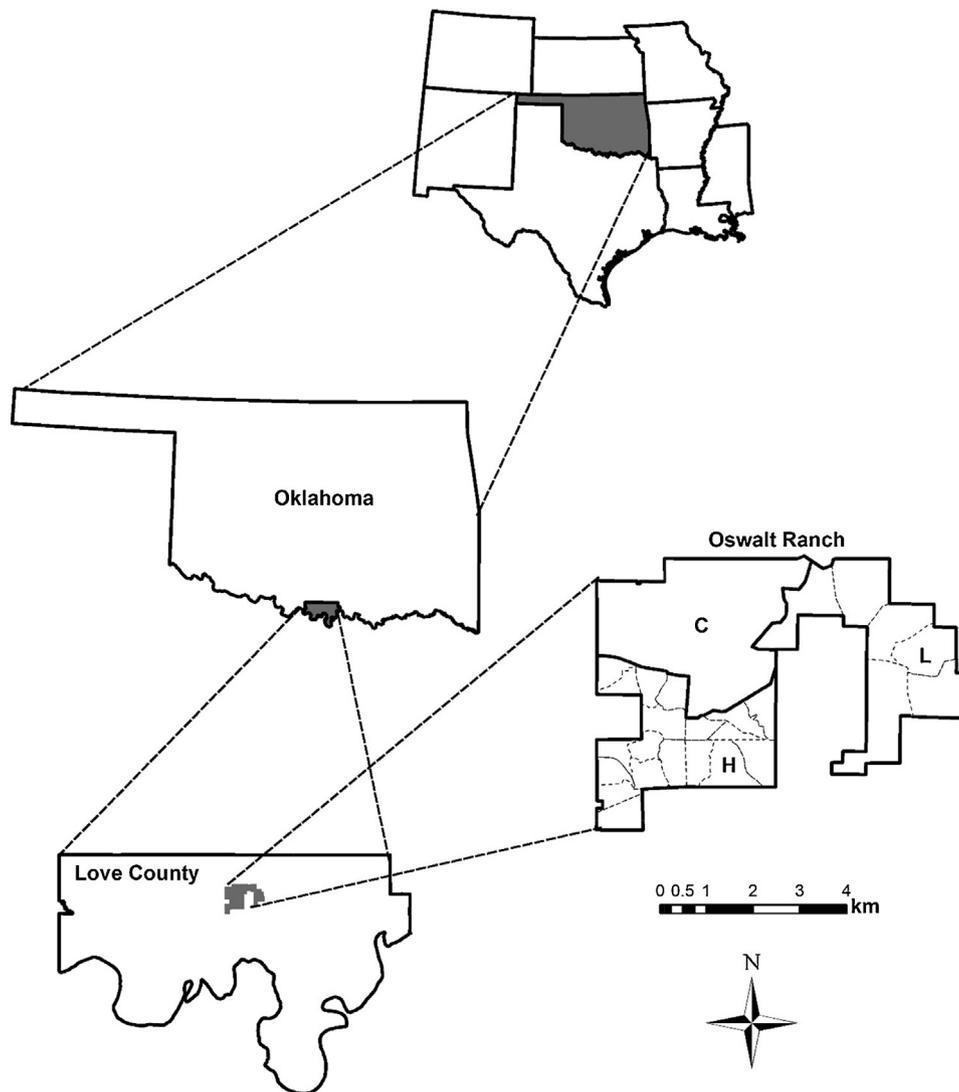
Fig. 1. The Samuel Roberts Noble Foundation Oswalt Ranch located in Love County, Oklahoma, USA. Risk treatment levels included no-risk (C; no hunters on 679 ha); low-risk (L; 1 hunter/101 ha; 586 ha); and high-risk (H; 1 hunter/30 ha; 583 ha). Risk treatments are displayed for 2008 but were randomized for 2009, which resulted in all treatments being shifted clockwise. Individual hunting compartments within risk treatments are represented by dashed lines, and the scale bar is representative of the Oswalt Ranch.

rangeland (Gee, Porter, Demarais, & Bryant 2011). During the study, NFOR did not conduct any cattle grazing or prescribed fire management. Lease hunting ($\bar{x} = 5$ hunters) ceased after the 2006 hunting season to minimize carryover effects of previous hunting exposure on study animals, and did not occur again until our study began in 2008. Hunters were not allowed to harvest collared deer to avoid reduction of sample size; however, an appropriate harvest environment was created by allowing the harvest of 20 female deer each year and 3 (2008) or 4 (2009) un-collared, antlered male deer each year. For a complete study area description see Appendix A.

Capture and handling

We used a modified drop-net system baited with corn (Gee, Holman, & Demarais 1999) to capture adult, male white-tailed deer during January–March in 2008 and 2009. We estimated age of deer according to tooth replacement and wear guidelines (Severinghaus 1949), but due to variations in wear patterns (Gee, Holman, Causey, Rossi, & Armstrong 2002), we classified deer as ≥ 1.5 years at capture; thus, all deer were ≥ 2 years of age at the beginning of the study period (November). We sedated deer with an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Kreeger 1996); thereafter, we weighed, inserted uniquely numbered ear tags, affixed each deer with a GPS collar (ATS G2000 Remote-Release GPS, Advanced Telemetry Systems, Isanti, MN), administered tolazine at 0.4 mg/kg as an antagonist to the xylazine, and released deer at site of capture. The Institutional Animal Care and Use Committee at Mississippi State University approved all capture, handling, and marking techniques (Protocol 07-034).

We programmed GPS collars to attempt a fix every 8 min from 7 November through the end of the study period each year (14 December 2008 and 13 December 2009). We monitored deer once monthly with traditional VHF telemetry from 1 February to 31 October (2008–2009) and once weekly from 1 November through end of rifle deer season (6 December 2008 and 7 December 2009) to determine general location of deer and mortality events.

Study design

To evaluate whether white-tailed deer alter their movement patterns to avoid recreational hunters, we conducted our study during the Oklahoma rifle deer season (i.e., 22 November–7 December 2008; and 21 November–6 December 2009); hunting was not allowed during other seasons (i.e., archery or muzzleloader). We divided the NFOR into three risk treatment areas based on existing landscape features, property boundaries, and cattle fencing to produce 3 areas of similar size (Fig. 1) and vegetation composition (i.e., forest, mixed shrubland/forest/grassland, and grassland). Risk treatments included no risk (control; 2008 = 679 ha; 2009 = 586 ha); low-risk (2008 = 586 ha; 2009 = 583 ha), and

high-risk (2008 = 583 ha; 2009 = 679 ha). The two hunted risk treatment areas resulted in hunter densities of 1 hunter/101 ha (low risk) and 1 hunter/30 ha (high risk). During the second year, the risk treatments were randomly assigned a new level of risk, which resulted in a clock-wise shift of treatments. For a complete description of risk treatments and assignment of hunters see Appendix A.

We evaluated the cumulative and longitudinal effects (time trend; $n = 36$ days) of risk of human activity between diurnal (06:00–18:00) and nocturnal periods (18:00–06:00). Over the 36-day study period, there were periods of risk and no risk: the risk exposure periods (length [days] of each period in parentheses) included pre-season (7 days), scouting (2 days), pre-hunt (4 days), hunt (16 days), and post-hunt (7 days; see Appendix A: Table 1). Pre-season had no hunting activity; the scouting period allowed hunters to enter the study area to learn hunting compartments and locate possible hunting sites; pre-hunt was a 4-day period immediately after scouting and in which no human activity was allowed on the study area; hunting season corresponded to the 16-day Oklahoma rifle season specified each year, with hunters distributed across the property based on risk level and compartment assignment (see above); and post-hunt immediately followed the rifle season, and again, there was no hunting activity during this time, although limited human activity occurred on portions of the study area (see Appendix A: Table 1). Last, data were partitioned based on temporal periods of risk, which consisted of a diurnal time period when risk was present on the landscape, and a nocturnal time period when risk and human activity ceased on the study area. Diurnal hours were defined as legal hunting hours (i.e., between 1/2 h before sunrise and 1/2 h after sunset) and nocturnal hours were defined as the hour after sunset through the hour before sunrise.

Movement behaviour

We evaluated the influence of risk treatment levels (i.e., no risk, low-risk, and high-risk), temporal period of risk (i.e., diurnal and nocturnal), and time (continuous variable; $n = 36$) on deer movement patterns using two metrics: movement rate (m/h) and relative displacement index (%). We calculated average hourly movement rate (m/h) by summing the total distance moved in an hour by individual deer for each risk treatment level, temporal period of risk, and time. We required ≥ 7 fixes/h, and for which all fixes fell within one risk treatment, to avoid negative bias in distance travelled (Little 2011). Next, we used a movement metric based on net displacement called relative displacement index (RDI, %; Dzialak, Olson, Webb, Harju, & Winstead 2015; see Appendix A: Fig. 1). RDI can be used to evaluate flight distance and site fidelity, as well as for assigning animals to behavioural or activity states (see Appendix A: Fig. 2). RDI was calculated for each 8-min fix and then averaged for each hour using only hours with ≥ 7 fixes/h that occurred within one risk treatment. For a complete description of movement metrics see Appendix A.

Table 1. Statistical results of movement distance (m/h) of male white-tailed deer in southern Oklahoma (2008 and 2009) from the 3-way analysis of variance (ANOVA) using generalized linear mixed models with 'year' and 'deer identification' as random effects in SAS® 9.3 (SAS Institute, Inc., Cary, NC).

Effect	Degrees of freedom		F-value	P-value
	Numerator	Denominator		
Day	1	18,075	792.19	<0.001
Treatment	2	15,453	0.13	0.874
Day × treatment	2	18,066	0.19	0.828
Diurnal/nocturnal	1	18,052	11.59	0.001
Day × diurnal/nocturnal	1	18,050	10.48	0.001
Treatment × diurnal/nocturnal	2	18,054	7.36	0.001
Day × treatment × diurnal/nocturnal	2	18,050	7.79	<0.001

Data analysis

We conducted three analyses to determine how behaviour of deer was affected by hunting intensity. First, we calculated the frequency of all GPS relocations across the 2 years combined to examine whether deer shifted distribution patterns relative to varying levels of risk (see methods in Appendix A; see results in Appendix B). Next, we examined the correlation between movement rate (m/h) and relative displacement index (RDI; %) to determine that the two movement metrics were describing different behaviours (see methods in Appendix A; see results in Appendix B). Last, we ran a 3-way analysis of variance to determine if movement rate and RDI were influenced by the main factors of risk treatment level ($n = 3$ levels), temporal period of risk ($n = 2$ levels), and time ($n = 36$ days modelled as a continuous variable); we also tested for all 2- and 3-way interactions using SAS® 9.3 (SAS Institute, Inc., Cary, NC). We used generalized linear mixed models (GLMM; GLIMMIX procedure) and specified deer identity and year as random effects (Gillies et al. 2006; Littell, Milliken, Stroup, Wolfinger, & Schabenberger 2006); year was modelled as a random versus fixed effect because of similar movement rates and trends across both years (Little et al., unpublished data). The Kenward–Roger denominator degrees of freedom adjustment (Kenward & Roger 1997) was used for testing the fixed effects and to account for random effects and correlated errors (Littell et al. 2006). We assessed the model residuals to monitor model performance. To compare differences of slopes for movement rate for each risk treatment level and temporal period of risk, we calculated z-scores and associated P-values (Paternoster, Brame, Mazerolle, & Piquero 1998). Sample sizes of deer in each risk treatment, risk exposure period, and year are provided in Appendix A: Table 2.

Results

Movement rate (m/h) was influenced by time ($P < 0.001$), temporal period of risk ($P = 0.001$), time × temporal period of risk ($P = 0.001$), and risk treatment level × temporal period of risk ($P = 0.001$; Table 1). However, there was a 3-way interaction among risk treatment level, temporal period of risk, and time ($F_{2,18050} = 7.79$, $P < 0.001$); therefore, we interpret all results relative to the 3-way interaction.

During the course of the 36-day study, movement rate declined across all risk treatment levels and temporal periods of risk but at different magnitudes (Fig. 2, Table 2). The greatest reduction in movement occurred for the low risk treatment during the night ($\beta = -7.966 \pm 0.591$ SE), followed by the control treatment at night ($\beta = -7.768 \pm 0.601$ SE), and the high risk treatment during the day ($\beta = -7.361 \pm 0.554$ SE; Fig. 2, Table 2). In general, movement rate was greatest in the low risk treatment during the night compared to all other risk treatments and periods of risk, and deer in the low and high risk treatments moved more than deer in the control treatment (Fig. 2). Movement rate in the high risk treatment during the day was greater at the beginning of the study compared to all risk treatments and temporal periods of risk except for the low risk treatment at night (Fig. 2). However, movement in the high risk treatment during the day culminated in lower movement rates than all other risk treatment levels; movement rate in the control treatment remained lower than all risk treatment levels (Fig. 2).

The magnitude of decrease in movement rate was similar for control and low risk treatments during diurnal ($z = 0.347$, $P = 0.364$) and nocturnal ($z = 0.235$, $P = 0.407$) periods (Fig. 2, Table 2). Movement rate declined at a greater rate ($z = 2.123$, $P = 0.017$) in the high risk treatment ($\beta = -7.361 \pm 0.554$ SE) during the day compared to the low risk treatment (-5.665 ± 0.575), but at night, movement rate declined faster ($z = -2.744$, $P = 0.003$) in the low risk treatment ($\beta = -7.996 \pm 0.591$ SE) than in the high risk treatment ($\beta = -5.660 \pm 0.598$ SE; Fig. 2, Table 2). Movement rate declined at a greater rate ($z = 2.578, P = 0.005$) in the high risk treatment ($\beta = -7.361 \pm 0.554$ SE) during the day compared to the control treatment ($\beta = -5.395 \pm 0.523$ SE), but at night, movement rate declined faster ($z = -2.487$, $P = 0.006$) in the control treatment ($\beta = -7.768 \pm 0.601$ SE) than in the high risk treatment ($\beta = -5.660 \pm 0.598$ SE; Fig. 2, Table 2). Additionally, we provided average movement rate (m/h) estimates for each temporal period of risk (i.e., diurnal and nocturnal),
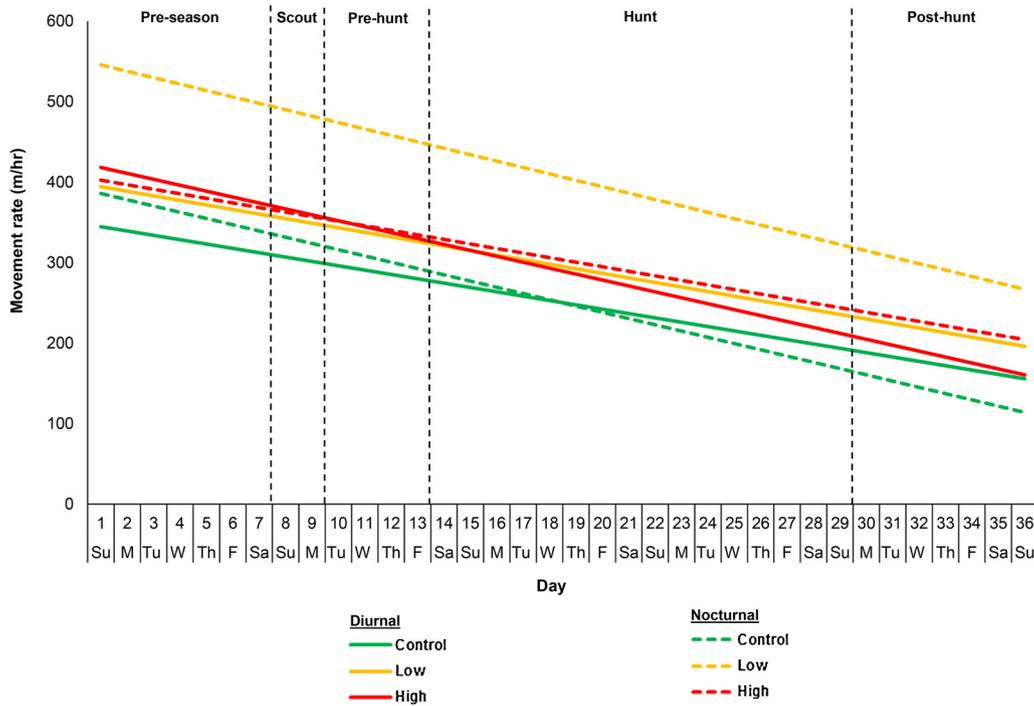
Fig. 2. Trends in average movement rate (m/h) of adult, male white-tailed deer in Love County, Oklahoma, USA across the 36-day study, combined and averaged across both years (2008 and 2009), as influenced by risk treatment level (i.e., no risk, low-risk, and high-risk) and temporal period of risk (i.e., diurnal and nocturnal). Year was modelled as a random effect because of similar movement rates and trends across both years. Vertical lines delineate the start and end of each risk exposure period as they relate to risk or no risk situations; however, a continuous variable to represent time was modelled to examine trends over time.

risk treatment level (i.e., no risk, low-risk, and high-risk), and risk exposure period (pre-season, scout, pre-hunt, hunt, and post-hunt) combination (see Appendix B: Table 1).

Relative displacement index (RDI) was only influenced by time ($F_{1,18574} = 25.05$, $P < 0.001$); all other main effects and interactions were not significant ($P \geq 0.144$; Table 3). RDI

declined over the 36-day study period ($\beta = -0.220 \pm 0.043$ SE), which is consistent with the metric that can capture longer term spatial processes on the landscape such as site fidelity. At the beginning of the study, deer covered larger areas as indicated by RDI (11.5%), culminating in a much lower level of displacement or space use at the end of the study

Table 2. Statistical comparisons for pairwise combinations of risk treatment level (no risk, lowrisk, and high-risk) and temporal period of risk (diurnal and nocturnal) to assess differences in slope for movement rate (m/h) of adult, male white-tailed deer (*Odocoileus virginianus*) in southern Oklahoma (2008 and 2009) across time using Z-tests. Significant comparisons are reported in italic font.

Risk treatment	Temporal period of risk	Slope	SE	Risk treatment	Temporal period of risk	Slope	SE	Z	P
Control	Day	−5.395	0.523	Control	Night	−7.768	0.601	2.977	*0.001*
Control	Day	−5.395	0.523	Low	Day	−5.665	0.575	0.347	0.364
Control	Day	−5.395	0.523	Low	Night	−7.966	0.591	3.257	*0.001*
Control	Day	−5.395	0.523	High	Day	−7.361	0.554	2.578	*0.005*
Control	Day	−5.395	0.523	High	Night	−5.660	0.598	0.333	0.370
Control	Night	−7.768	0.601	Low	Day	−5.665	0.575	−2.529	*0.006*
Control	Night	−7.768	0.601	Low	Night	−7.966	0.591	0.235	0.407
Control	Night	−7.768	0.601	High	Day	−7.361	0.554	−0.498	0.309
Control	Night	−7.768	0.601	High	Night	−5.660	0.598	−2.487	*0.006*
Low	Day	−5.665	0.575	Low	Night	−7.966	0.591	2.791	*0.003*
Low	Day	−5.665	0.575	High	Day	−7.361	0.554	2.123	*0.017*
Low	Day	−5.665	0.575	High	Night	−5.660	0.598	−0.006	0.497
Low	Night	−7.966	0.591	High	Day	−7.361	0.554	−0.747	0.228
Low	Night	−7.966	0.591	High	Night	−5.660	0.598	−2.744	*0.003*
High	Day	−7.361	0.554	High	Night	−5.660	0.598	−2.086	*0.018*

Table 3. Statistical results of relative displacement index (RDI; %) of male white-tailed deer in southern Oklahoma (2008 and 2009) from the 3-way analysis of variance (ANOVA) using generalized linear mixed models with 'year' and 'deer identification' as random effects in SAS® 9.3 (SAS Institute, Inc., Cary, NC).

Effect	Degrees of freedom		F-value	P-value
	Numerator	Denominator		
Day	1	18,574	25.05	<0.001
Treatment	2	2203	0.25	0.782
Day × treatment	2	18,615	0.06	0.941
Diurnal/nocturnal	1	22,566	2.13	0.144
Day × diurnal/nocturnal	1	22,564	1.10	0.295
Treatment × diurnal/nocturnal	2	22,570	0.69	0.500
Day × treatment × diurnal/nocturnal	2	22,568	0.65	0.520

(RDI 3.8%), a reduction of three times the initial movement pattern. Additionally, we provided average relative displacement index (%) estimates for each temporal period of risk (i.e., diurnal and nocturnal), risk treatment level (i.e., no risk, low-risk, and high-risk), and risk exposure period (pre-season, scout, pre-hunt, hunt, and post-hunt) combination (see Appendix B: Table 1).

Discussion

White-tailed deer exhibited behavioural adaptations to varying levels of hunter risk across the study area. Deer made both temporal and spatial decisions to potentially avoid contact with hunters. Deer reduced their distance travelled and increased site fidelity (i.e., the relative displacement index decreased) over the course of the study during diurnal and nocturnal hours despite the breeding season occurring during the study period. Deer also were affected spatially by the presence of hunters; overall distribution of collared deer subtly shifted use to the control area during diurnal hours once hunting season started (see Appendix B: Fig. 1). Movement also was greater in the 2 risk treatments compared to the control area. Therefore, despite deer adjusting movement behaviour temporally (decreased movement and displacement over time), deer were still disturbed by hunter risk across the landscape, which resulted in subtle redistribution and escape-type of movement behaviour when the probability of coming into contact with a hunter increased during the day. Deer generally had greater movement rates during the nocturnal period when within the two risk treatments compared to the diurnal period, which may suggest that deer adjusted behaviours to safer times, albeit movement decreased over time for all treatment groupings. However, on a nearby study area with minimal to no hunting pressure, diurnal movements of deer were greater compared to nocturnal movements (Webb, Gee, Strickland, Demarais, & DeYoung 2010).

There is much disparity in the literature on how hunters affect behaviour of game animals, especially white-tailed deer. Some of this disparity may stem from study design, or lack thereof, the availability of habitat (e.g., security cover),

style of hunting by hunters (e.g., still, drive or stalk hunts), whether the area is private or public, and the density of hunters. This study occurred on private land where density of hunters was controlled. In the low risk treatment, hunter effort was 0.05 and 0.17 h/ha/day in the high risk treatment (Little et al. 2014). Most other studies reported greater hunter effort than even our high risk treatment. For example, hunter effort varied from 0.57 h/ha/day (Rhoads et al. 2013) to 1.31 h/ha/day during firearms season (Root et al. 1988). Hunter effort in this study was much lower than that previously recorded, but we did observe temporal and spatial changes in movement behaviour. Compared to other studies, and assuming all factors are equal except for hunter effort, we may have observed behavioural modifications because we were able to consistently maintain hunter pressure over the firearms hunting season, which is relatively short (16 days) compared to other states' firearms hunting season where hunting pressure is distributed over longer periods of time.

Diurnal and nocturnal movement rate and relative displacement declined over the course of the study even though movements are expected to increase during the breeding season. In another big game species, human hunting activity did not influence movement behaviour of moose (*Alces alces*; Neumann, Ericsson, & Dettki 2009). Conversely, hunting caused elk to increase movement rates (Cleveland et al. 2012). Besides the negative trend over time, we also observed that one of the sharpest declines in movement occurred in the high risk treatment during day time, as we would predict because this area would be the riskiest to deer. Deer responded temporally to risk and at two spatial scales. First, deer in all risk treatments reduced movement, indicating that even deer in control treatment recognized risk. Second, deer in the low and high risk treatments responded to risk by travelling at faster rates. The trend for decreased movement and displacement considers the general effect of hunting, which can be considered to cover a broader spatial scale than the individual risk treatments. Because male deer maintain relatively large home ranges (Webb, Hewitt, & Hellickson 2007; Hellickson, Campbell, Miller, Marchinton, & DeYoung 2008; Foley et al. 2015), most deer likely came into contact (i.e., close proximity) with hunters at some time during the study; therefore,

deer probably were not naïve to risk on the landscape. For deer to decrease movements and increase site fidelity (i.e., the relative displacement index decreased) indicates that deer used smaller areas more intensively, likely because they were familiar with them and could escape detection by predators. Had deer not taken this confined movement strategy, deer may have been more vulnerable to harvest because moving prey are more easily detected (Lima & Dill 1990; Cleveland et al. 2012), which we found to be the case in this population (Little et al. 2014).

We partitioned the data into diurnal and nocturnal periods to assess two periods: presence of human predation risk and no presence of human predation risk. We also qualitatively compared results from this study to a nearby study area that used intensive tracking of white-tailed deer during the hunting season, and where hunting pressure was minimal to non-existent (Webb, Riffell, Gee, & Demarais 2009; Webb et al. 2010). On a nearby study area, movement distance was greatest during diurnal hours (Webb et al. 2010). However, we did not find greater movements during the day in the present study when deer were within the two risk treatments. Regardless of temporal period of risk, movement rate was greater in the risk treatments compared to the control treatment, but movement was still elevated at night, especially in the two risk treatments. This could indicate that deer could not perceive the lack of human predation risk across the landscape when the risk was removed at night time. Another explanation is that these movement behaviours may indicate that deer were making behavioural trade-offs during the day. Deer were disturbed in the two risk treatments during the day, causing them to move greater distances than deer in the control treatment, but deer still had elevated movements at night because deer had to make trade-offs between avoiding risk and other fitness producing activities (e.g., browsing, breeding, etc.) during the day. Therefore, at night, deer may have continued to have elevated movements to make up for lost time foraging or breeding during the day. If this hypothesis is true, then deer in the presence of risk may be at a greater disadvantage than their counterparts that do not have to face a landscape of fear (Laundré, Hernández, & Ripple 2010). Deer exposed to risk then would have greater energy requirements (Christianson, Liley, & Winnie 2007) because they expend more energy to avoid risk (in this study, during the day and in the two risk treatments) and then expend energy while foraging at night, all while faced with the intense rigours of breeding activities that further cause deer to expend energy and lose body mass (Hewitt 2011). Therefore, it is unknown how long exposure to risk and changes in behaviour and energy acquisition will influence individual fitness, or population health and productivity; though exposure to risk from hunting likely has minimal effect on long-term fitness and productivity given the short duration that hunters are afield each year relative to natural predators in our study.

Movement rate declined over the course of the study, even in the presence of the breeding season. Peak of conception occurred on 30 November with a range from 4 November to 24 December in south-central Oklahoma (Webb et al. 2009). During the breeding season, male deer typically increase movements in search of receptive does (Webb et al. 2010; Foley et al. 2015). The lack of an increase in movement distance around the peak of conception, could mean that the risk of predation from hunters had a stronger influence on movement than the breeding season. For any study, it is important to know when the breeding season occurs to at least qualitatively assess the data or quantitatively test for an effect. Sargent and Labisky (1995) also discuss how the breeding season can confound interpretation of results if the breeding season occurs during the hunting season and goes unquantified. Other analyses found that including a covariate for days before or after peak conception was not significant (A.R. Little, unpublished data). As an example, Karns et al. (2012) also observed a decrease in movement distance from pre-hunt to hunt periods, but attributed, at least partially, this change to the fact that the breeding season occurred during the pre-hunt period, whereas post-breeding occurred during the hunt. Contrary to our findings, moose breeding season had a greater impact on movement behaviour than hunting, which most likely was below a threshold that would cause moose to alter their behaviour (Neumann et al. 2009). Although hunting pressure on our study area was lower than those previously reported in the literature, the presence of risk on our study area appeared to induce a response by deer whereby risk contributed more strongly to altering movement behaviour than the breeding season.

After the hunting season, movement distance and relative displacement of deer continued to decrease despite the fact that human predation risk was no longer a threat across the landscape, and the end of the peak breeding range was still occurring (Webb et al. 2009). We do note that we modelled a time trend over the 36-day study, but raw data of movement rate for each day also showed similar results (i.e., reduced movement). We would predict that over the 7-day post-hunt period, deer would increase movements back to pre-hunt levels, especially in the presence of the breeding season. Because movements did not increase during the post-hunt exposure period may indicate that deer were still experiencing carry-over effects from the hunting season that made them more cautious to avoid risk. This is a likely scenario given an intense 16-day hunting season. In other situations, such as on public land or states where the hunting season is extended over months, this pattern may in fact change, where movements would increase after the hunting season if hunting pressure was less intense. In more intense hunting situations, we would predict the same trend as observed herein.

Conclusions

As urbanization and habitat fragmentation increases, and populations of large carnivores decrease across North America, researchers and land managers must continue to monitor the effects of human activity on behavioural ecology of

wildlife species. In particular, harvest by humans is the primary population management tool used to control deer numbers. Therefore, hunting by humans provides a potential mechanism that biologists can employ to create risk effects across the landscape, which can alter the spatial distribution and behaviour of game species (Cromsigt et al. 2013). In summary, early season hunting will have the greatest potential to achieve harvest numbers because observation rates and potential for harvest will be at their peaks because deer have not yet learned to avoid humans, and thus have not altered their behaviour temporally or spatially.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.12.003.

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Appendix A

Study area

3   Predominant plant species on the Noble Foundation's Oswalt Ranch included various

4   oaks (*Quercus* spp.), elms (*Ulmus* spp.), hickories (*Carya* spp.), ashes (*Fraxinus* spp.),

5   hackberries (*Celtis* spp.), osage orange (*Maclura pomifera*), bluestems (*Andropogon spp.*),

6   switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), gramas *(Bouteloua* spp.),

7   dropseeds *(Sporobolus* spp.), Texas wintergrass *(Stipa leucotricia*), and numerous forbs.

8   Invasive species were present, including old world bluestem (*Bothriochloa ischaemum*), jointed

9   goatgrass (*Aegilopis cylindrica*), bromes (*Bromus* spp.), and eastern red cedar (*Juniperus*

10   *virginiana*). The NFOR is rurally located with minimal paved, gravel, and dirt roads (density =

11   1.4 km/km^2). Elevation ranges from 233 to 300 m, and slope ranges from 0 to 41 degrees.

12   During the study period (i.e., hunting season), rainfall was 0.07 cm in 2008 and 0.2 cm in 2009;

13   average daily temperature was 6.48° and 7.51° C in 2008 and 2009, respectively (Burneyville,

14   OK; Oklahoma Mesonet; www.mesonet.org). Coyote (*Canis latrans*) and bobcat (*Lynx rufus*)

15   occurred on the study area and were potential natural predators of white-tailed deer (primarily

16   fawns).

17   **Methods**

18   **Study design**

19   Risk treatment areas were further divided into hunting compartments to distribute hunters

20   across the landscape at the appropriate density of hunters in each risk treatment. For example, in

21   2008, the low-risk treatment was divided into 6 hunting compartments (1 hunter/101 ha) while

22   the high-risk treatment was divided into 19 hunting compartments (1 hunter/30 ha; Fig. 1). An

23   individual hunter was then assigned to each single compartment for that rifle deer season. To

24   help maintain specified risk treatment effects, we required that hunters spend ≥4

25   hours/day/compartment, resulting in hunters spending an average of 0.05 hunter-hours/ha/day in

26   the low-risk treatment and 0.17 hunter-hours/ha/day in the high-risk treatment (Little et al. 2014).

27   Surrounding properties had a variety of hunting effort applied each year, ranging from none to an

28   equivalent of our high-risk treatment (R. Williams, The Samuel Roberts Noble Foundation,

29   personal communication). However, we could not control or accurately document hunter

30   densities on all surrounding properties.

31   **Movement behaviour**

32   The relative displacement index (RDI; Dzialak et al. 2015) is based on net displacement,

33   or the straight-line distance between the starting location for an individual and subsequent

34   locations along the movement path of that individual (Turchin 1998). Net displacement was

35   calculated within each individual's movement path as

36    $$\sqrt{\{(UTMe_l - UTMe_1)^2\} + \{(UTMn_l - UTMn_1)^2\}}$$

37   where *UTMe* and *UTMn* are respective easting and northing coordinates of location data (datum:

38   North American Datum 1983; and projection: Universal Transverse Mercator zone 14 north), 1 is

39   the first GPS location in the path, and *l* is each subsequent location in the path. We calculated
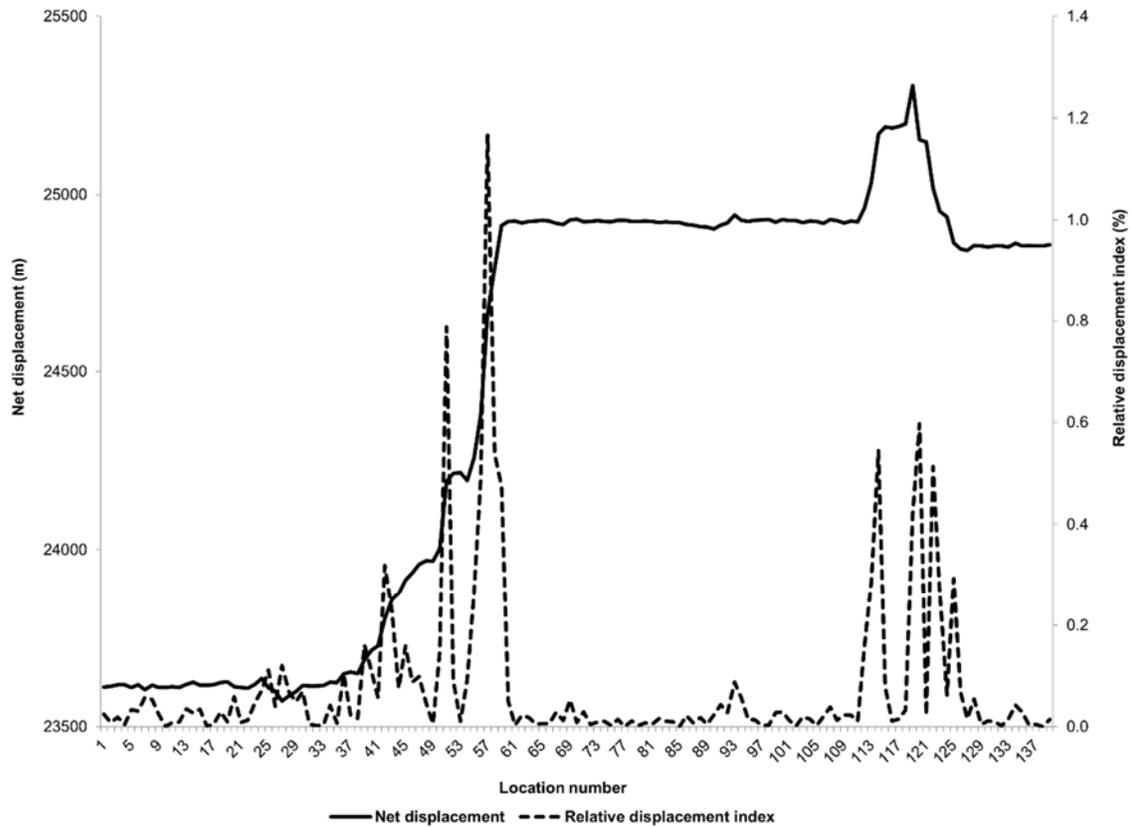
40   the relative displacement index as

41    $$|\{(net\ displacement_{l+1} - net\ displacement_l) \div net\ displacement_l\} \times 100|$$

42   which quantifies the relative change in amplitude of net displacement between location *l* and

43   location *l* + 1. RDI follows the absolute value of net displacement, where high RDI values

44   correspond to high net displacement values, and low RDI values correspond to small changes in

45   net displacement (Fig. 1). Refer to Dzialak et al. (2015) for further information. However, RDI

46   has several advantages over net displacement. First, to determine the displacement of an

47   individual from one time step to the next, net displacement must be interpreted through

48   visualizations (Fig. 1, y-axis #1), whereas RDI does not. Second, the meaning of net

49   displacement, which is based on the starting location in the data set, does not allow for the

50   assessment in change of location between subsequent time steps; however, RDI allows for

51   interpretation of the relative change in position. Last, RDI is a relative measure (%) in proximal

52   change in the area used, which allows the raw RDI values to be interpreted and plotted for

53   thresholds in displacement and used to place animals into behavioural states such as 1) local or

54   stationary behaviour, 2) within patch movements, 3) between or among patch movement, and 4)

55   flight or dispersal movement (Fig. 2).

56   **Analysis**

57   To determine whether movement distance (m/hr) and RDI were correlated, we ran a

58   Pearson correlation in SAS® 9.3 (SAS Institute, Inc., Cary, NC) (see results in Appendix B). We

59   also ran a frequency analysis to determine the number of locations within each treatment and

60   season for diurnal and nocturnal periods separately using the FREQ procedure in SAS® 9.3. We

61   used this analysis to assess whether deer were shifting use of treatments across periods to

62   relocate to safer areas away from human predation risk (see Appendix B: Fig. 1).

63

64   **Fig. 1.** Net displacement (m; y-axis 1) and relative displacement index (%; y-axis 2). Example

65   of an adult male white-tailed deer during hunting season in Love County, Oklahoma, USA; Fig.

66   shows the relationship between net displacement and relative displacement index.
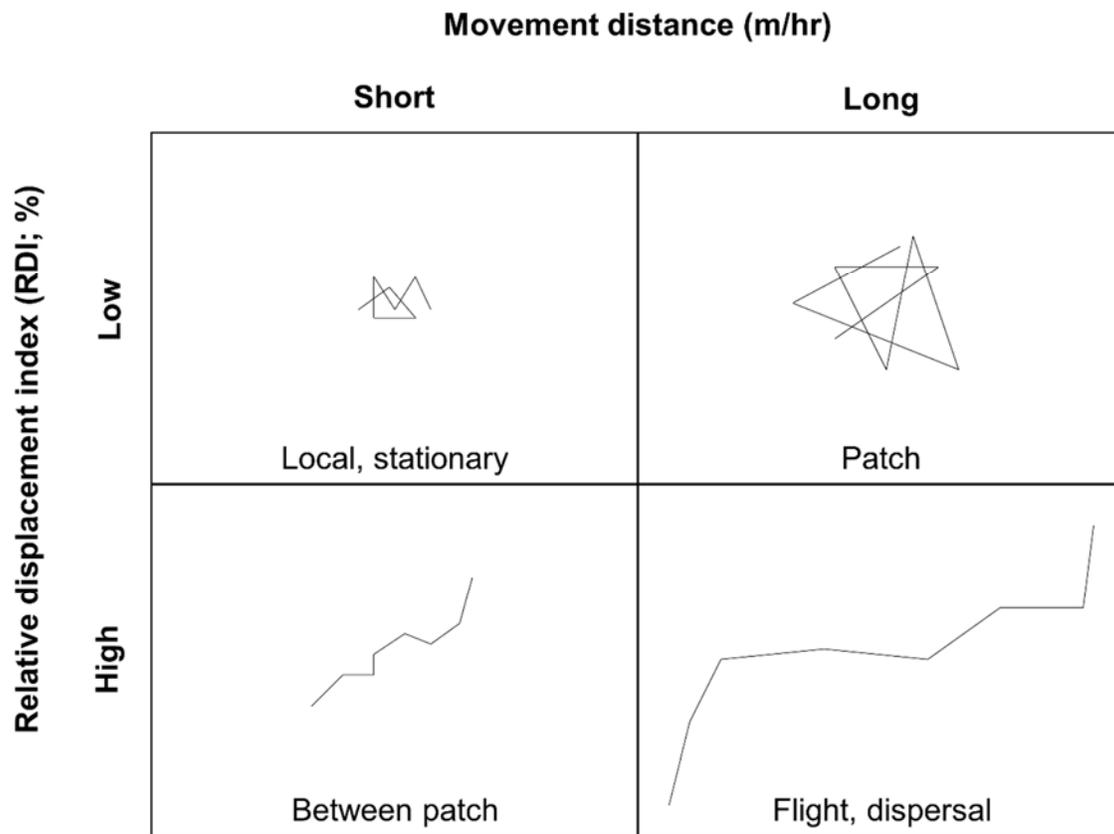
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Movement distance (m/hr)

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75 **Fig. 2.** Conceptual interpretation of two movement metrics: movement distance (m/hr) and

76 relative displacement index (%). The relative displacement index, when interpreted along with

77 movement distance, can be used to assign behavioural states to animals.

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84   **Table 1.** Dates for risk exposure periods during the 2008 and 2009 study periods. 'Risk present'

85   either indicates that human activity or risk was ('Yes') or was not ('No') occurring across the

86   study area. Note that although we define risk exposure periods, movement parameters were

87   modeled using a time trend model to assess the temporal trend over time.

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

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89

90   **Table 2.** Sample size of deer by risk exposure period and risk treatment level during 2008 and

91   2009 on the Oswalt Ranch in southcentral Oklahoma, USA. Some deer used multiple treatments

92   during the course of the season, so sample size reflects the total number of deer in each treatment

93   at any point during the season.

Risk exposure period[a]	Risk treatment[b]	Year	n
Pre-season	Control	2008	12
		2009	9
	Low	2008	10
		2009	13
	High	2008	11
		2009	13
Scout	Control	2008	12
		2009	6
	Low	2008	9
		2009	9
	High	2008	10
		2009	13
Pre-hunt	Control	2008	12
		2009	7
	Low	2008	8
		2009	12
	High	2008	10
		2009	11
	Control	2008	12

Period	Treatment	Year	Value
Hunt		2009	8
	Low	2008	7
		2009	10
	High	2008	12
		2009	15
Post-hunt	Control	2008	8
		2009	7
	Low	2008	5
		2009	8
	High	2008	8
		2009	8

94 ᵃRisk exposure period: Pre-season (2008: 9–15 November; 2009: 8–14 November), scout (2008:
95 16–17 November; 2009: 15–16 November), pre-hunt (2008: 18–21 November; 2009: 17–20
96 November), hunt (2008: 22 November–7 December; 2009: 21 November–6 December), and
97 post-hunt (2008: 8–14 December; 2009: 7–13 December).
98 ᵇRisk treatment levels: Control = no risk; low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30
99 ha.

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110   **References**

111   Dzialak, M. R., Olson, C. V., Webb, S. L., Harju, S. M., & Winstead, J. B. (2015). Incorporating

112   within- and between-patch resource selection in identification of critical habitat for

113   brood-rearing greater sage-grouse. *Ecol. Processes, 4(5),* 1–15.

114   Little, A. R., Demarais, S., Gee, K. L., Webb, S. L., Riffell, S. K., Gaskamp, J. A., & Belant, J.

115   L. (2014). Does human predation risk affect harvest susceptibility of white-tailed deer

116   during hunting season? *Wildl. Society Bull., 38,* 797–805.

117   Turchin, P. (1998). *Quantitative Analysis of Movement: measuring and modeling population*

118   *redistribution in plants and animals.* Sunderland, MA: Sinauer Associates.

1 **Appendix B**

2 **Results**

3   We deployed 52 collars (25 in 2008, 27 in 2009) on adult, male deer during the study.

4 However, we analyzed data from 19 collars in 2008 and 18 collars in 2009, which included seven

5 individuals collared during both years. Fifteen deer were excluded because of illegal harvest (n =

6 8), legal harvest on a neighboring property prior to pre-season in our study (n = 1), mechanical

7 failure of the collar (n = 3), natural mortality (n = 1), deer-vehicle collision (n = 1), and dispersal

8 (n = 1). One of the 8 illegally harvested deer required the development of an underwater

9 telemetry antenna to retrieve the collar from a pond (Webb et al. 2011); we retrieved all data

10 from the collar. GPS collars averaged 96.8% (SD = 9.8) fix success, and 3.7 m error (SD = 7.6)

11 (Little 2011).

12   We found low correlation ($r = 0.259$) between movement distance (m/hr) and relative

13 displacement index (RDI); therefore, we proceeded to analyze the two movement variables

14 separately because they described different movement processes. We also assessed how the

15 distribution of deer changed during the course of the study and relative to risk treatments. The

16 number of days differed within each temporal risk exposure period (i.e., season); therefore, we

17 only make qualitative comparisons of the use of risk treatments within each risk exposure period.

18 We found some apparent differences between diurnal (Fig. 1A) and nocturnal (Fig. 1B) temporal

19 periods of risk. During nocturnal periods, deer used low and high risk treatments slightly greater

20 (~1.5-4%) than the control treatment during the pre-season, scout and hunt periods; use of the

21 three risk treatments were similar during the hunt risk exposure period, but use in the control

22 treatment was marginally greater (~2-2.5%) than the low and high risk treatments during post-

23 hunt (Fig. 1B). During diurnal hours of the pre-season, there was slightly greater use within each

24   of the risk treatments (1.5-4%) compared to the control treatment (Fig. 1). However, once

25   hunting season started, the control treatment received greater use (~4-8.5%) compared to the

26   individual use of the risk treatments; we found this same pattern during the post-hunt period (Fig.

27   1) where use of the control treatment was 3.5-5.5% greater than the two risk treatments.

28   **Discussion**

29   A primary advantage of this project was the experimental nature of the study design with

30   both spatial and temporal controls. A control treatment was used to assess spatial differences

31   among risk treatment levels, albeit the control treatment was in close proximity to the risk

32   treatments. A temporal control was included by sampling deer intensively (1 GPS location every 8

33   min) prior to the start of hunting season to serve as a baseline reference. The study also was

34   replicated for two years, with risk treatment levels being randomized during the second year to

35   avoid any carryover or cumulative effects. We had strict control over assignment of hunters to

36   treatments that allowed us to maintain appropriate density of hunters across the low and high risk

37   treatments. Hunters were randomly assigned to risk treatments, and then to compartments within

38   treatments. Without random assignment of hunters to compartments and treatments, we may have

39   introduced systematic bias into the study because some hunters were more successful in finding

40   and observing deer (Little et al. 2014). For these reasons, the inferences made from this study will

41   be stronger than traditional, observational types of studies where control over study design and

42   hunter participation is lacking.

43   Despite the controlled nature of this study, we would make recommendations for future

44   study design and for accounting for uncontrollable factors. Having used only one study area for all

45   3 risk treatments, we would recommend using 3 separate study sites to avoid any carryover effects

46   of risk treatments on the control treatment; each study site would be randomly assigned a risk

47   treatment level and conducted for three years to allow all sites to be assigned to each of the three

48   risk treatment levels (i.e., assuming 3 treatments as in this study). We also could not control

49   hunting pressure on surrounding properties. Although hunting occurred on most surrounding

50   properties, it is unknown how outside hunting pressure affected deer on our study site. We

51   recommend that future researchers obtain a measure of hunting pressure on surrounding properties

52   to be included as a covariate into statistical modeling (i.e., to adjust for the time deer are off the

53   study site and on neighboring properties with varying levels of pressure). We also could not control

54   illegal harvest, which is common within the white-tailed deer's range (Haines et al. 2012). In total,

55   8 deer were illegally harvested either out-of-season, over the legal bag limit, outside of legal

56   shooting hours, or on private property where the hunter did not have permission. These data

57   indicate that risk of illegal harvest occurs in many forms and at many times, which cannot be

58   controlled.

A)

Diurnal

B)
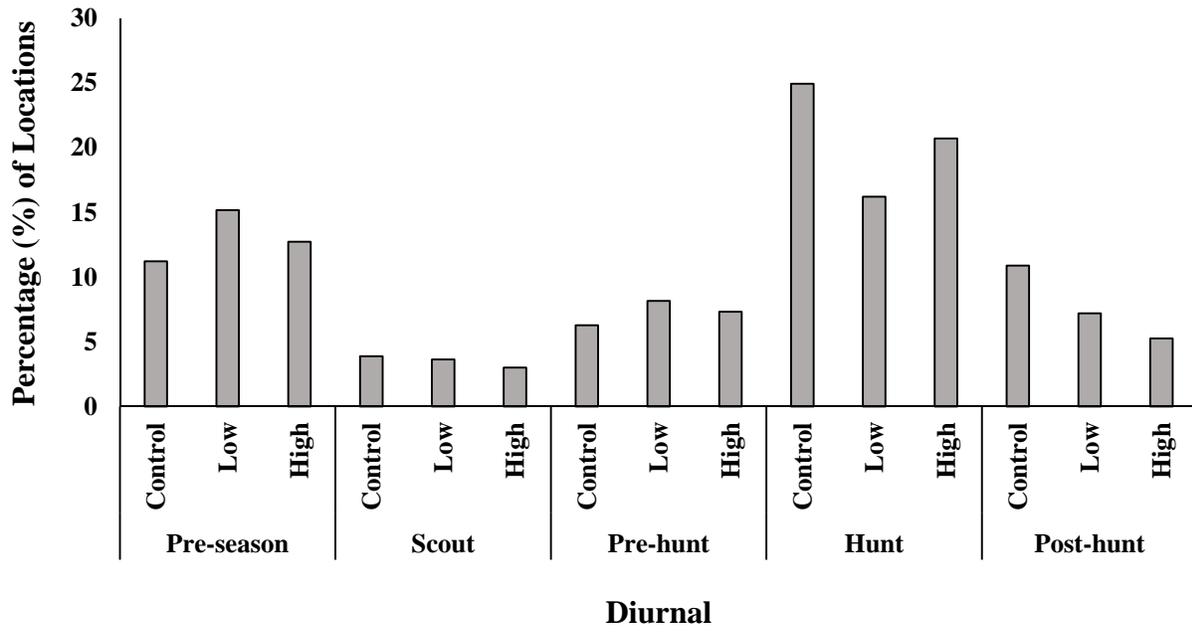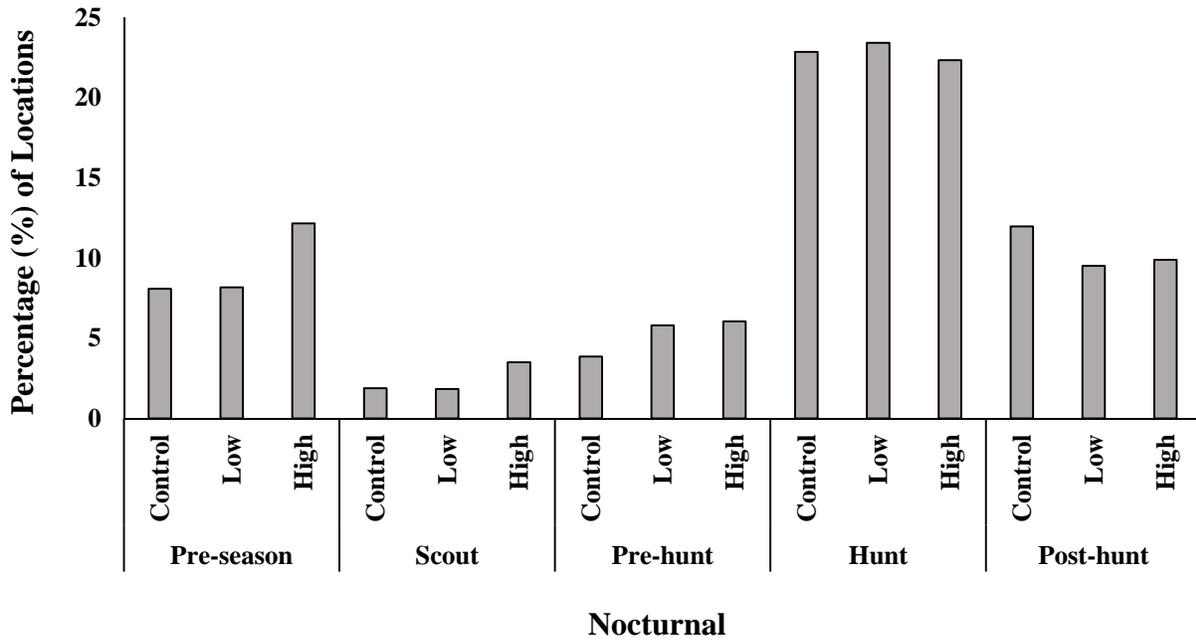
Nocturnal

Fig. 1. Percentage of all deer locations across risk treatment levels and risk exposure periods for diurnal (A) and nocturnal (B) temporal exposures of risk (summarized across 2008 and 2009) to depict temporal patterns of distribution across the study area.

Table 1. Mean (± SE) movement distance (m/hr) and relative displacement index (%)for each temporal period of risk (i.e., diurnal and nocturnal), risk treatment level (i.e., no risk, low-risk, and high-risk), and risk exposure period (pre-season, scout, pre-hunt, hunt, and post-hunt) combination. The study was conducted during 2008 and 2009 on the Oswalt Ranch in Love County, OK, USA, which is owned and operated by The Samuel Roberts Noble Foundation.

DN	Treat	Risk Exposure Period	Movement Distance		Relative Displacement Index	
			Mean	SE	Mean	SE
Diurnal	Control	Pre-season	305.9	37.3	3.2	0.5
		Scout	355.2	92.6	3.6	0.8
		Pre-Hunt	439.9	48.9	4.2	0.6
		Hunt	303.1	59.7	3.2	0.4
		Post-Hunt	146.1	18.0	2.0	0.4
	Low	Pre-season	363.3	37.6	4.1	0.6
		Scout	412.6	71.2	3.6	0.7
		Pre-Hunt	310.6	32.5	3.8	0.5
		Hunt	390.0	65.8	4.1	0.7
		Post-Hunt	248.8	64.4	2.9	0.7
	High	Pre-season	368.0	36.7	4.0	0.4
		Scout	429.0	59.5	4.5	0.7
		Pre-Hunt	419.8	47.0	4.0	0.5
		Hunt	343.2	57.6	3.7	0.5

		Post-Hunt	179.7	18.4	2.2	0.6
Nocturnal	Control	Pre-season	334.8	47.8	3.4	0.6
		Scout	278.3	19.5	3.4	0.6
		Pre-Hunt	370.7	45.5	4.3	0.9
		Hunt	249.7	22.7	2.3	0.3
		Post-Hunt	146.4	16.2	1.9	0.4
	Low	Pre-season	582.2	94.5	5.3	0.6
		Scout	361.5	48.0	4.2	1.0
		Pre-Hunt	442.3	69.8	5.2	0.8
		Hunt	321.9	45.0	3.5	0.5
		Post-Hunt	213.1	42.6	2.5	0.6
	High	Pre-season	376.7	33.6	4.7	0.4
		Scout	404.2	65.6	4.4	0.6
		Pre-Hunt	350.3	46.5	4.1	0.7
		Hunt	264.0	24.8	3.1	0.3
		Post-Hunt	229.2	31.7	2.7	0.4

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