Papers in Natural Resources   Natural Resources, School of

2014

Does Human Predation Risk Affect Harvest Susceptibility of White-Tailed Deer During Hunting Season?

Andrew R. Little
Mississippi State University, alittle6@unl.edu

Stephen Demarais
Mississippi State University, steve.demarais@msstate.edu

Kenneth L. Gee
The Samuel Roberts Noble Foundation,

Stephen L. Webb
The Samuel Roberts Noble Foundation, slwebb@noble.org

Samuel K. Riffell
Mississippi State University, sriffell@cfr.msstate.edu

See next page for additional authors

Follow this and additional works at: http://digitalcommons.unl.edu/natrespapers

Part of the Natural Resources and Conservation Commons, Natural Resources Management and Policy Commons, and the Other Environmental Sciences Commons

Authors

Andrew R. Little, Stephen Demarais, Kenneth L. Gee, Stephen L. Webb, Samuel K. Riffell, Joshua A. Gaskamp, and Jerrod L. Belant

Does Human Predation Risk Affect Harvest Susceptibility of White-Tailed Deer During Hunting Season?

Andrew R. Little,[1] Stephen Demarais,[1] Kenneth L. Gee,[2] Stephen L. Webb,[1] Samuel K. Riffell,[1] Joshua A. Gaskamp,[2] and Jerrold L. Belant,[3]

1 Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762

2 The Samuel Roberts Noble Foundation, 2510 Sam Noble Parkway, Ardmore, OK 73401

3 Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Mississippi State, MS 39762

Corresponding author — A. R. Little, email alittle139@gmail.com

Present address for K. L. Gee — 6438 Gene Autry Road, Ardmore, OK 73401, USA
Present address for S. L. Webb — The Samuel Roberts Noble Foundation, 2510 Sam Noble Parkway, Ardmore, OK 73401, USA

Abstract

Large carnivores are considered a primary source of mortality for many ungulate populations, but harvest by hunters is the primary means of population management. However, research is needed to evaluate how human predation risk influences observability (a surrogate to harvest susceptibility) of ungulates. We determined how hunting intensity and duration influence observation rates of white-tailed deer (*Odocoileus virginianus*) and how deer behavior (i.e., movement rate and resource selection) affects observation rates. We sampled 37 adult (≥2 yr) male deer at 2 levels of risk (i.e., low-risk = 1 hunter/101 ha; and high-risk = 1 hunter/30 ha) during 3 exposure periods (i.e., first, second, and third weekend of hunting) on a 1,861-ha property in Oklahoma, USA, during the 2008 and 2009 rifle deer-seasons. Observation rates (collared deer/hunter-hr/day) were greatest during the first weekend in both the low- and high-risk treatments, but declined each weekend thereafter in

both treatments. Immediately prior to hunter observation, movement rate of observed collared deer was greater than that of unobserved collared deer, but only when hunting risk was high. Greater movement rates of deer in the high-risk treatment also led to a greater probability of observation. Hunters also had a greater probability of observing collared deer at higher elevations. Overall, deer modified their behavior to avoid detection by hunters. These results can be used to explain decreased observation rates to hunters and to modify harvest rates by altering timing and intensity of human predation risk during the recreational hunting season to help achieve population management goals through harvest.

Keywords: animal behavior, hunting, observability, *Odocoileus virginianus*, Oklahoma, movement, resource selection

Large carnivores can play an important role in direct regulation of ungulate populations (Skogland 1991, Laliberte and Ripple 2004, Beschta and Ripple 2009), but in many systems, humans have replaced large predators as the greatest source of annual mortality of most large mammals (Collins and Kays 2011). Simultaneously, predators also can indirectly (i.e., predation risk) influence ungulate populations by altering fitness-linked behaviors (e.g., movements; Altendorf et al. 2001, Pierce et al. 2004, Valeix et al. 2009) through effects on reproduction or survival (Creel et al. 2007). With an increasingly human-dominated landscape, human predation risk caused by recreational hunting may play an important role in behavioral modification of ungulate populations (Laliberte and Ripple 2004). For example, white-tailed deer (*Odocoileus virginianus*) observations declined as the recreational hunting season progressed (Grau and Grau 1980). However, research is needed to address whether declining observations (a surrogate to harvest susceptibility) are influenced by human predation risk thereby affecting population abundance estimates based on hunter observation data.

In increasingly human-dominated landscapes, programs based on adaptive-management principles are becoming more important to effectively manage wildlife (Rutledge and Lepczyk 2002). This change requires information on the effects of humans on wildlife behavior to make more informed scientific-based management decisions. Wildlife can alter their behaviors in the presence of humans by changing their movements and shifting resource selection (Proffitt et al. 2009; Dzialak et al. 2011*c*; Webb et al. 2011*a,b*; Ciuti et al. 2012; Cleveland et al. 2012). These changes can have important management consequences for wildlife biologists and land managers in dynamic landscapes where humans and deer coexist (Decker and Chase 1997, Conover 2002, Messmer 2009). For example, Kilpatrick et al. (2002) observed deer using dense patches of cover and areas unoccupied by hunters as refuges to avoid the risk of hunter harvest in an urban setting. Such areas may

allow deer to reduce the risk of predation, which may further increase the difficulties of effective deer management. Gaining knowledge on ungulate response to recreational hunters can enable biologists to make more cost-effective investments for management when resources are limited.

Evidence is accumulating that the behavior of individual animals can influence individual-specific demographic outcomes (e.g., survival, reproduction, etc.), which has been observed across taxa (e.g., elk [*Cervus elaphus*], Dzialak et al. 2011*c*; greater sage-grouse [*Centrocercus urophasianus*], Dzialak et al. 2011*b*). Adult woodland caribou (*Rangifer tarandus caribou*) avoided areas with increased levels of natural predation by shifting habitat use (McLoughlin et al. 2005). White-tailed deer likely follow a similar pattern during the hunting season by modifying their behavior to avoid encounters with recreational hunters through changes in movement (Abrams 2000, Sih and McCarthy 2002) or use of selected landscape features (e.g., vegetation cover, elevation, slope, and roads; Kilgo et al. 1998, Ripple and Beschta 2004, Sawyer et al. 2006, Dzialak et al. 2011*a*, Webb et al. 2011*a*). Some deer may be observed more often when using certain vegetation communities or landscape features (Sage et al. 1983), whereas some deer may avoid detection through changes in movement behavior (Root et al. 1988). Altered behavior potentially could lead to an under- or overestimation of ungulate population abundance when based on hunter observation data.

To address the effects of humans on wildlife behavior, we focused our study on white-tailed deer, one of the most widely hunted big-game animals in North America (Halls 1973). Our first objective was to evaluate how hunting intensity and duration influence observation rate (a surrogate to harvest susceptibility). We hypothesized that observation rate would be greater under high hunting pressure, but that it would decline temporally, particularly under high hunting pressure, as deer increasingly perceived hunters as a threat. Our second objective was to evaluate how movement rate and habitat selection affect observation rate at 2 levels of risk (i.e., low- and high hunting pressure). We hypothesized that the probability of observing a given deer would increase with greater movement rate and in open areas, at higher elevations, on flatter terrain, and near roads where visibility for hunters would be greatest, especially under high hunting pressure. Finally, we characterized hunter success based on deer observation rates. Our study was designed to better understand susceptibility of deer to observation and potential harvest, with implications for harvest management and using hunter observations for evaluating ungulate population abundance.
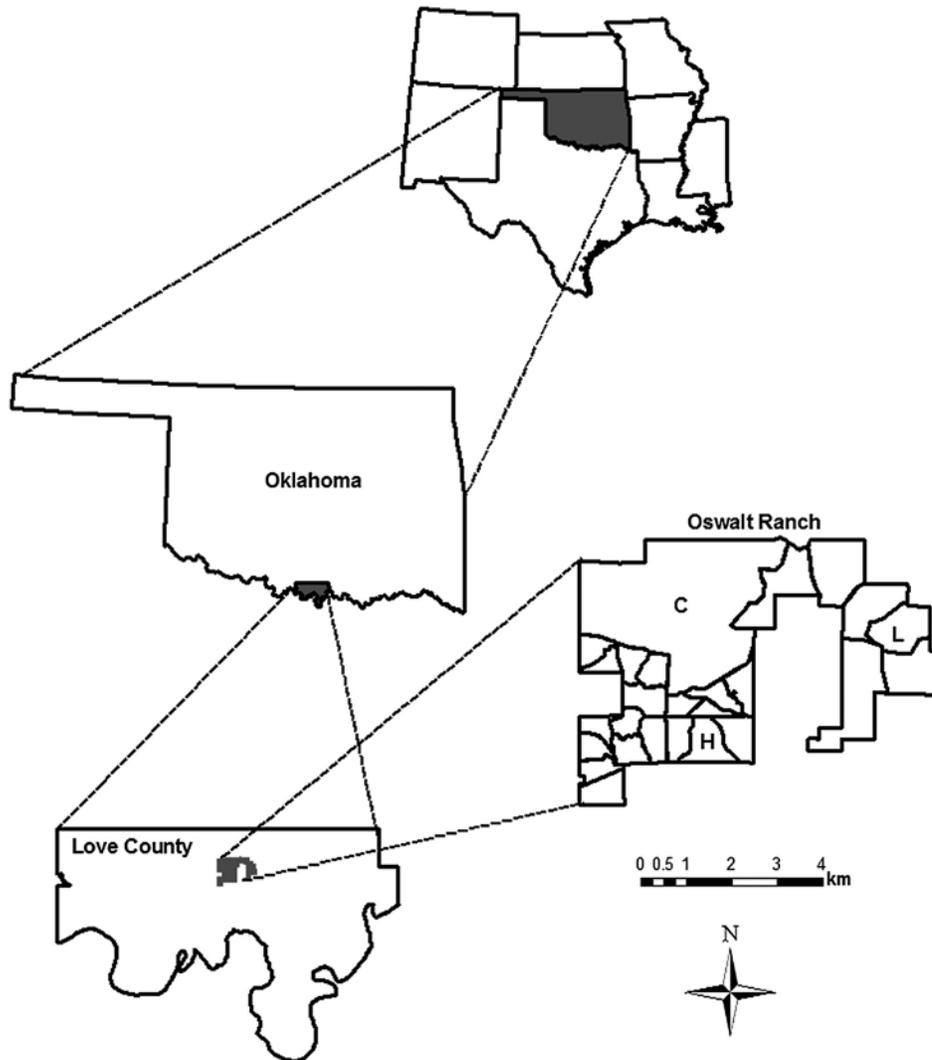
Figure 1. The Samuel Roberts Noble Foundation Oswalt Ranch located in Love County, Oklahoma, USA. White-tailed deer hunting treatments were no-risk (C; no hunters on 679 ha); low-risk (L; 1 hunter/101 ha; 586 ha); and high-risk (H; 1 hunter/30 ha; 583 ha). Treatments are displayed for 2008 but were randomized for 2009, which resulted in all treatments being shifted clockwise. Scale bar is representative of Oswalt Ranch.

Study Area

We conducted this study on The Samuel Roberts Noble Foundation's Oswalt Ranch (NFOR) in Love County, Oklahoma, USA (**Fig. 1**). The NFOR was a 1,861-ha ranch located in the Cross Timbers and Prairies eco-region, which was characterized by a mixture of wooded areas (e.g., various oaks [*Quercus* spp.], elms [*Ulmus* spp.], and hickories [*Carya* spp.]), bottomlands (e.g.,

various oaks; ashes [*Fraxinus* spp.], elms, hackberries [*Celtis* spp.], and osage orange [*Maclura pomifera*]), and openings (e.g., mixture of bluestems [*Andropogon* spp.], switchgrass [*Panicum virgatum*], Indiangrass [*Sorghastrum nutans*], and numerous forbs; Gee et al. 2011). Invasive species were present, including Old World bluestem (*Bothriochloa ischaemum*), jointed goatgrass (*Aegilops cylindrica*), and bromes (*Bromus* spp). Shallow upland sites were common and were dominated by gramas (*Bouteloua* spp.), bluestems, dropseeds (*Sporobolus* spp.), and Texas wintergrass (*Nassella leucotricha*). The NFOR was a rural landscape with minimal paved, gravel, and dirt roads (density=1.4 km/km2). Elevation ranged from 233 m to 300 m and slope ranged from 0° to 41°. During the 2008 and 2009 Oklahoma rifle deer-season (2008 = 22 Nov–7 Dec; and 2009 = 21 Nov–6 Dec), total rainfall was 0.07 cm and 0.61 cm, respectively. Average daily temperature during the rifle deer-season was 6.71 °C in 2008 and 7.19 °C in 2009 (Burneyville, OK; Oklahoma Mesonet; www.mesonet.org). During the study, NFOR was a non-operational ranch without any cattle grazing or prescribed fire management. Lease hunting ($\bar{x}$ = 5 hunters) was restricted after the 2006 hunting season to minimize carry-over effects of previous hunting exposure on study animals. Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) occurred on the study area and were potential predators of white-tailed deer.

Methods

Hunter Assignment

To evaluate whether white-tailed deer alter their behavior to avoid recreational hunters, we conducted our study during the Oklahoma rifle deer-season. Hunting was not allowed during any other season. We divided the NFOR into 3 treatment areas based on existing landscape features, property boundaries, and fencing, with the goal of producing 3 areas of similar size (Fig.1) and vegetation composition (i.e., forest, mixed forest/ grassland, and grassland). In 2008, treatments included no hunting pressure (control, 679 ha; hereafter, no-risk); low hunting pressure (1 hunter/101 ha, 586 ha; hereafter, low-risk), and high hunting pressure (1 hunter/30 ha, 583 ha; hereafter, high-risk). To create temporal replication for the second year, the treatment areas were randomly assigned a new level of risk, which resulted in a clock-wise shift of treatments. Hunt treatments were divided into individual hunting compartments to achieve the required treatment levels. For example, in 2008, the low-risk treatment area was divided into 6 hunting compartments, while the high-risk treatment area was divided into 19 hunting compartments. An individual hunter was then assigned to each single compartment for that rifle deer-season. To maintain the specified treatment effects, we required hunters to spend ≥ 4 hours/day/compartment during the

weekend; the periods when participation would likely be the greatest. Hunters were not allowed to harvest collared deer to avoid reduction in the sample size; however, an appropriate harvest environment was created by allowing the harvest of 20 antlerless and 3 mature, un-collared antlered deer each year, except in 2009 when hunters were allowed to harvest 4 mature, un-collared antlered deer. Surrounding properties had annual hunting efforts ranging from none to an equivalent of our high-risk category (R. Williams, The Samuel Roberts Noble Foundation, personal communication); however, we could not control or accurately document hunter pressure on surrounding properties.

Capture and Handling

We used modified drop-net systems baited with corn (Gee et al. 1999) to capture adult, antlered 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 because of variations in wear patterns (Gee et al. 2002), we classified them as ≥ 1.5 years at capture; thus, all deer were ≥ 2 years of age at the beginning of the study period (Nov). We sedated deer with an intramuscular injection of telazol (4.4 mg/kg) and xylazine (2.2 mg/kg; Kreeger 1996); thereafter, we weighed each deer, inserted into each deer a uniquely numbered ear tag, fitted each deer with a global positioning system (GPS) collar (ATS G2000 Remote-Release GPS; Advanced Telemetry Systems, Isanti, MN), and administered tolazine to each deer at 0.4 mg/kg (0.5 intramuscularly and 0.5 intravenously) as an antagonist to the xylazine. Deer were released at point 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 minutes from 7 November through the end of the study period each year. We monitored deer once per month with traditional very high frequency telemetry from 1 February to 31 October (2008–2009) and once per week from 1 November through end of rifle deer-season (6 Dec 2008 and 7 Dec 2009) to determine general location of deer and mortality events.

Prey Exposure

Prey may have the ability to discriminate between changes in magnitude and temporal variation in risk (Lima and Steury 2005). Therefore, we evaluated the effect of low and high human predation risk during 3 temporal periods of the Oklahoma rifle deer-season: weekend 1 (22–23 Nov 2008, 21–22 Nov 2009), 2 (28–30 Nov 2008, 27–29 Nov 2009), and 3 (6–7 Dec 2008, 5–6 Dec 2009); Friday was included into the second weekend because low- and high-risk treatments were achieved. The property was open to hunting during other days of the Oklahoma rifle deer-season with the exception of

Wednesdays and Thanksgiving. When hunters were present on weekdays, average hunter effort (i.e., hunter hr/ ha/day) in the low- ($\bar{x}$ = 0.004, SE = 0.002) and high-risk ($\bar{x}$ = 0.025, SE = 0.009) treatments was minimal.

Hunter Observations

We required hunters to record start and end times of their activities within the assigned hunting compartment, number of collared antlered deer, and number of un-collared antlered and antlerless deer observed as a surrogate to harvest susceptibility. Hunters recorded ear-tag color, number, and time of collared antlered deer sightings. Hunters carried a Garmin Etrex Venture GPS unit (Garmin, Olathe, KS) to track their locations, with a fix attempted every minute. To ensure correct identification of collared deer, we included only hunter observations that occurred during legal shooting hours (i.e., between one-half hour before sunrise and one-half hour after sunset), and validated hunter observations of deer using GPS locations of deer and hunters within ArcGIS 9.3. To determine the number of deer available for hunter observation, we overlaid the deer GPS locations over both hunted treatments during legal shooting hours each day during the Oklahoma rifle deer-season, and identified individual deer available for hunter observation.

Spatial Ecology of Deer

To address what factors affect the probability of observing a given deer, we compared time-specific location parameters (i. e., movement rate and resource selection) of observed and unobserved collared deer across hunt treatments. To assess how deer behavior influences the probability of observation, we used the time of a given observation and the GPS fixes to determine each deer's location during the closest 8-minute location immediately prior to that observation for all observed and unobserved collared deer. To account for hunter recording errors of the exact time of observation and to accurately describe deer activity prior to the recorded observation, locations were required to fall within 5– 30 minutes prior to hunter observation. For example, if deer 58 was observed at 0705 hours, we used the location prior to the observation (e.g., 0658 hr) and classified it as observed. For all unobserved deer during the same time period as observed deer (within 30 min of the observation), we chose the closest temporal location and classified it as unobserved.

Movement rate and resource selection.—To evaluate behavioral variation that may influence observation susceptibility, we compared movement rates and resource selection of observed and unobserved collared deer. We calculated movement rates by calculating the linear distance between 2 successive fixes (i.e., 8-min interval) using the Animal Movement extension within Hawth's Tools in ArcGIS 9.3 (Beyer 2004). We then divided movement distance by 8 minutes (m/min) and multiplied by 60 to obtain mean distance

(m) moved per hour (hereafter, movement rate). For example, if deer 58 was observed at 0705 hours, we used the distance between the location at 0658 hours and 0706 hours (i.e., 328 m) and divided the value by 8 minutes to obtain 41 m/minute. We then multiplied this value by 60 to obtain 2,460 m moved/hour.

To evaluate resource selection at time of observation for all observed and unobserved collared deer, we re-sampled a 1-m-resolution aerial image from the U.S. Department of Agriculture-Geospatial Data Gateway (2008) into a 17-m image using ERDAS Imagine 9.3 (ERDAS, Inc., Atlanta, GA) software. We chose this grid size because it is the smallest patch size perceived by white-tailed deer (Webb et al. 2009) and encompassed most GPS error ($\bar{x}$ = 3.7 m, SD = 7.6; Little 2011). We classified vegetation into 3 categories: forest, mixed forest–grassland (hereafter, mixed), and grassland. Forested areas were considered to have ≥70% closed canopy cover, grasslands contained ≥70% open areas, and mixed had <70% forest and <70% grassland. To validate landscape classifications from remotely sensed data, we measured visual obstruction at 30 randomly placed vegetation plots within each cover type using a 1.8-m Nudds density board (Nudds 1977). The board was viewed from a distance of 10 m in each cardinal direction from a height of 1.5 m and obstruction of each of the 6 sections was estimated in 20% increments. Finally, we obtained a 10-m-resolution digital elevation model from the U.S. Department of Agriculture-Geospatial Data Gateway (2010) to calculate elevation (m) and slope (°) using Spatial Analyst in ArcGIS 9.3.

We extracted values for each vegetation type (i.e., forest, mixed, and grassland), elevation, and slope for each observed and unobserved collared deer location using Intersect to Point within Hawth's Tools (Beyer 2004). In addition, we delineated roads (i.e., dirt, gravel, and paved) bounding and within the study area that hunters used to travel to and from their hunting compartments. These roadways received greatest traffic during early morning and evening hours when hunters were entering and leaving the field. Using ArcGIS 9.3, we spatially linked each collared deer location to the nearest roadway to evaluate whether distance to the nearest roadway affects observation of collared deer.

Statistical Analysis

Descriptive statistics.—We measured hunter effort using hunter-hours/ha/day and measured hunter success using collared deer observed/hunter-hours/day and minutes/deer observation. We calculated hunter-hours/ha/day to document differences in hunter effort between low- and high-risk treatments. To calculate hunter-hours/ha/day, we totaled the number of hours hunted each day within each treatment during the 3 weekends, and then divided hours hunted by treatment size and number of days. Collared deer/hunter-hour/day describes the number of collared deer (i.e., including

repeated observations of the same deer) observed each day relative to amount of hunter effort expended. To calculate collared deer/hunter-hour/day, we divided the number of collared deer observed by hunter-hours/day during each weekend. We calculated mean deer observation rate as number of minutes required to observe any deer (both collared and un-collared deer) by each hunter. This index of hunter success also indicated deer susceptibility to harvest. We calculated coefficient of variation (CV) to describe how repeatable individual hunters were in their ability to observe deer in general (i.e., all collared and un-collared deer).

Logistic regression.—To determine factors that influenced the probability of observing a collared deer, we used a hierarchical variable inclusion approach. We used generalized linear mixed models (GLMM; PROC GLIMMIX) and a logistic regression framework. Because of small sample size of observations, we combined 2008 and 2009 data. We analyzed the observational data as a binary response variable (1 = observed; 0 = unobserved). We included deer identity, year, and a deer × year interaction as random effects to account for variation and correlation among measurements that may be affected by individual deer behavior (i.e., deer identity) or annual differences. For the GLMM, we used a binary distribution, logit-link function and a variance components covariance structure for random effects. We incorporated all factors (i.e., hunting treatment, movement rate, vegetation type, elevation, slope, and distance to road) as main effects into a full model, including a continuous covariate (Julian date) to account for declining observation rates over time. We then removed all variables with $P \geq 0.100$, resulting in a simplified basic model to which we added an interaction term between hunting treatment and movement rate to assess whether the relationship between observation probability and movement rate differed between treatments. Elevations were similar between treatments; therefore, we did not include an interaction term between hunting treatment and elevation (Little 2011). We considered this our final model from which we made inferences.

Results

We deployed 52 collars (25 in 2008, 27 in 2009) on adult, antlered deer during the study. However, we analyzed data from 19 collars in 2008 and 18 collars in 2009, which included 7 individuals collared during both years. Fifteen deer were excluded from analysis because of illegal harvest ($n = 8$), legal harvest on neighboring property ($n = 1$), mechanical collar failure ($n = 3$), natural mortality ($n = 1$), deer–vehicle collision ($n = 1$), and dispersal ($n = 1$). We used 364 individual 8-minute inter-fix intervals (observed = 47; unobserved = 317) prior to the recorded hunter observation times to examine

the spatial ecology of observed and unobserved deer. Global positioning system collars averaged 96.8% (SD = 9.8) fix success (Little 2011).

Prey Exposure and Hunter Effort

Hunter effort averaged 0.05 hunter-hours/ha/day in the low-risk treatment and 0.17 hunter-hours/ha/day in the high-risk treatment. Hunter effort declined 20% from the first to the third weekend of hunting in both treatments: low-risk declined 0.05–0.04 hunter-hours/ha/day and high-risk declined 0.20–0.16 hunter-hours/ha/day. However, hunters continued to provide substantial risk during the second and third weekends of hunting, with 0.05 and 0.16 hunter-hours/ha/day spent afield in the low- and high-risk treatments, respectively.

Hunter Observations

Hunters in the low-risk treatment observed 4 out of 14 (28.6%) collared deer available to be observed during the first weekend. Of the 4 deer, 3 were observed once and 1 was observed twice. In contrast, hunters in the high-risk treatment observed 9 out of 17 (53.0%) collared deer available to be observed. Of the 9 deer, 2 were observed once, 3 twice, 1 three times, 2 four times, and 1 five times. During the second weekend, hunters in the low-risk treatment observed 4 out of 13 (30.8%) individual collared deer. All 4 collared deer were observed once. Hunters in the high-risk treatment observed 8 out of 15 (53.3%) collared deer during the second weekend. Of the 8 collared deer observed, 5 were observed once, 1 twice, and 2 were observed 3 times. Hunters in the low-risk treatment observed 1 out of 11 (9.1%) collared deer available to be observed during the third weekend. The only deer observed was observed one time. Conversely, hunters in the high-risk treatment did not observe any of the 12 deer available to be observed.

Hunter observation rates were similar between low- and high-risk treatments despite a 3-fold difference in hunter effort between treatments. Number of observations of collared deer/hunter-hour/day in the low-risk treatment declined 83% across the 3 weekends (first: $\bar{x}$ = 0.053, SE = 0.025; second: $\bar{x}$ = 0.019, SE = 0.014; and third weekends: $\bar{x}$ = 0.009, SE = 0.009). Hunter observations in the high-risk treatment declined by 64% between weekends 1 and 2. No collared deer were observed in the high-risk treatment during the last weekend of the rifle deer-season.

Although the overall mean observation rate was 353 min/ deer, some hunters were more successful than others in observing collared and un-collared deer. The top 25% of hunters observed a deer every 200 minutes, while hunters in the lowest 25% required >475 minutes to observe a deer (**Fig. 2**). Additionally, some hunters were consistently (CVs < 60%) successful in observing deer during each outing, whereas other hunters consistently observed fewer deer (CVs < 60%; Fig. 2).
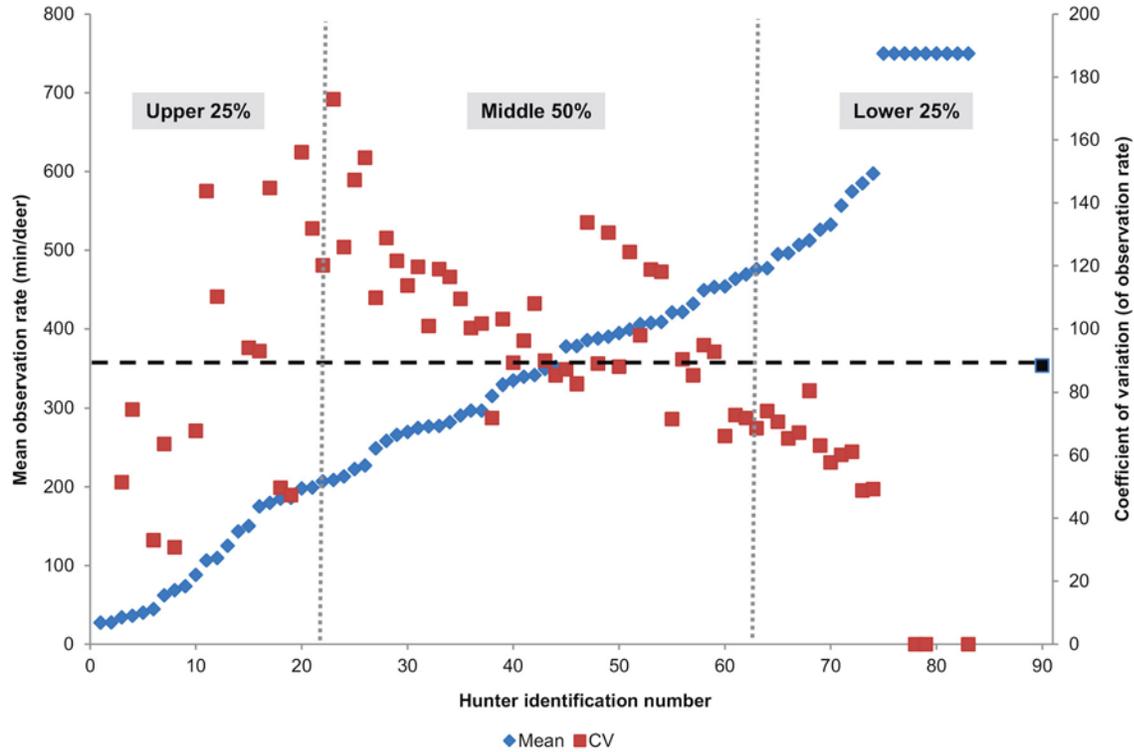
Figure 2. Mean observation rates (min/deer observation on left-hand *y*-axis) of all antlered and antlerless white-tailed deer (*Odocoileus virginianus*) observed by hunters (*n* = 83) during each hunting outing (i.e., morning hunt, evening hunt, or all day) on the Samuel Roberts Noble Foundation Oswalt Ranch located in Love County, Oklahoma, USA, during the rifle–firearm seasons of 2008 (22 Nov–7 Dec) and 2009 (21 Nov–6 Dec). Hunters were ranked in order of most successful (i.e., fewest minutes required to observe deer) to least successful (i.e., most minutes required to observe deer). Gray, dashed vertical lines separate the 25% most successful hunters ("Upper 25%") from average hunters ("Middle 50%") and the least successful hunters ("Lower 25%"). The coefficient of variation (for hunters with multiple hunting outings) is displayed as red squares on right-hand *y*-axis as a measure of how consistent hunters were in observing deer during each outing. The black square (at far right) represents the mean observation rate of all hunters, along with corresponding reference line (black, dashed horizontal line).

Spatial Ecology of Deer

Our final model from which we made inferences included an interaction term for movement rate × treatment and elevation. The probability of observing a collared deer was influenced by the movement rate × treatment interaction ($F_{1,328} = 10.07$, $P = 0.002$). That is, the probability of detecting a deer increased with increasing movement rate in the high-risk treatment, but not

in the low-risk treatment ($F_{1,328}$ = 17.5, P < 0.001); mean movement rate of observed deer (1,161.8 m/hr ± 146.8 SE) was 146.5% greater than that of unobserved deer in the high-risk treatment (471.3 m/ hr ± 43.5 SE). In contrast, movement rate did not affect the probability of a deer being observed in the low-risk treatment (t_{328} = –0.15, P = 0.880); distance travelled by deer in the low-risk treatment averaged 742.1 m/hour (± 99.9 SE). Although the covariate Julian date was not significant ($F_{1,328}$ = 1.77, P = 0.184), we retained it in the model to adjust for declining observation rates over time. The probability of observing a collared deer was also influenced by elevation ($F_{1,328}$ = 3.50, P = 0.062). Hunters had a greater probability (0.026 ± 0.014 SE) of observing collared deer at higher elevations.

Discussion

Our findings indicate that deer altered their behavior temporally during the Oklahoma rifle deer-season to avoid interaction with hunters, thereby influencing susceptibility to harvest. As hypothesized, hunters observed a greater absolute number of collared deer in the high-risk treatment compared with the low-risk. However, intensity of hunting (low- and high-risk) did not influence susceptibility to harvest on a per hunter basis. Greater movements of observed deer in the high-risk treatment suggest that movement behavior is an important predictor of harvest susceptibility at higher risk levels.

Our study design provided a strong framework to evaluate the role that human predation risk has on observation rates (a surrogate to harvest susceptibility) and factors influencing susceptibility of deer to harvest based on behavioral measures. We were able to control human predation risk across a large landscape (comparable, or larger than most landholding sizes where recreational hunting activities occur), collect fine-scale spatial data on hunters and deer, randomize treatment assignments, and repeat the study for 2 years. Furthermore, random assignment of hunters to compartments in each hunted treatment distributed successful and unsuccessful hunters. We suggest that others use manipulative experiments for future studies that evaluate varying levels of risk on animal behavior. This suggestion stems from the fact that previous studies found minimal or insignificant changes in deer behavior during the hunting season (Root et al. 1988, Kilgo et al. 1998, Karns et al. 2012), which may be due to the fluidity of hunter numbers and/or limited hunting pressure on other study areas.

One aspect that we could not control was hunting activity on surrounding properties and illegal deer harvest. Illegal harvest is prevalent across the white-tailed deer's range (Haines et al. 2012), as well as on and around our study area. During the course of this study, 8 deer were illegally harvested (e.g., out of season, over the legal bag limit, outside of legal shooting hours,

or on private property where the hunter did not have permission). One illegal harvest, and subsequent disposal of the GPS collar into a pond, required the development of an underwater telemetry probe to find and recover the lost collar, and associated data (Webb et al. 2011*c*). Illegal harvest is a pervasive issue facing many wildlife managers. A major concern to hunters and land managers is that antlered deer passed up on their property will be harvested, either legally or illegally, on an adjacent property. Our data suggest that some antlered deer may be at risk for harvest on surrounding properties or by illegal harvest. Therefore, management programs should focus on managing for deer across neighboring properties (e.g., cooperatives) to account for risk of harvest on adjacent properties with different management plans and/or illegal harvest. Managers also may want to consider illegal harvest when setting harvest quotas to avoid overharvest of the antlered segment of the deer herd.

Observation rates among treatments declined following the first weekend of hunting as deer learned that hunters posed a threat in a form similar to predation risk. This decline is consistent with previous studies that found a similar decline in white-tailed deer observations after exposure to risk (Murphy 1965, Van Etten et al. 1965, Grau and Grau 1980). Although hunters in the high-risk treatment observed a greater absolute number of deer, the similar number of collared deer observed/hunter-hour/day indicates that high-risk levels did not increase observation rates over time. This suggests that adult deer can perceive human predation risk and make behavioral changes to reduce the probability of encounter. Similar to Grau and Grau (1980), our results suggest that maintaining a high level of human predation risk will not increase the probability of observing deer over time. In fact, observation rates declined over time.

Changing human predation risk and duration of risk could be used to facilitate harvest management. However, if increased harvest is desired, identifying successful hunters may help meet harvest quotas; our results indicate some hunters will be more successful in harvesting deer because they are better at observing deer, and do so consistently. However, we did not account for hunter behavior (style of hunting, movement, treatment, time of day, compartment, etc.) in these results, which likely influenced whether hunters were successful at observing deer.

Although the primary focus of this study was on collared, antlered deer, we conducted a *post hoc* analysis to determine whether observations of unmarked antlered and antlerless deer revealed similar trends in declining observations over time. We recorded the total number of antlered and antlerless deer observed each day by treatment and plotted the mean number of deer observed/day (*y*-axis) over time (*x*-axis). Observations of antlered and antlerless deer declined across both treatments as the hunting season progressed (**Fig. 3**A,B). However, number of deer observed in the high-risk
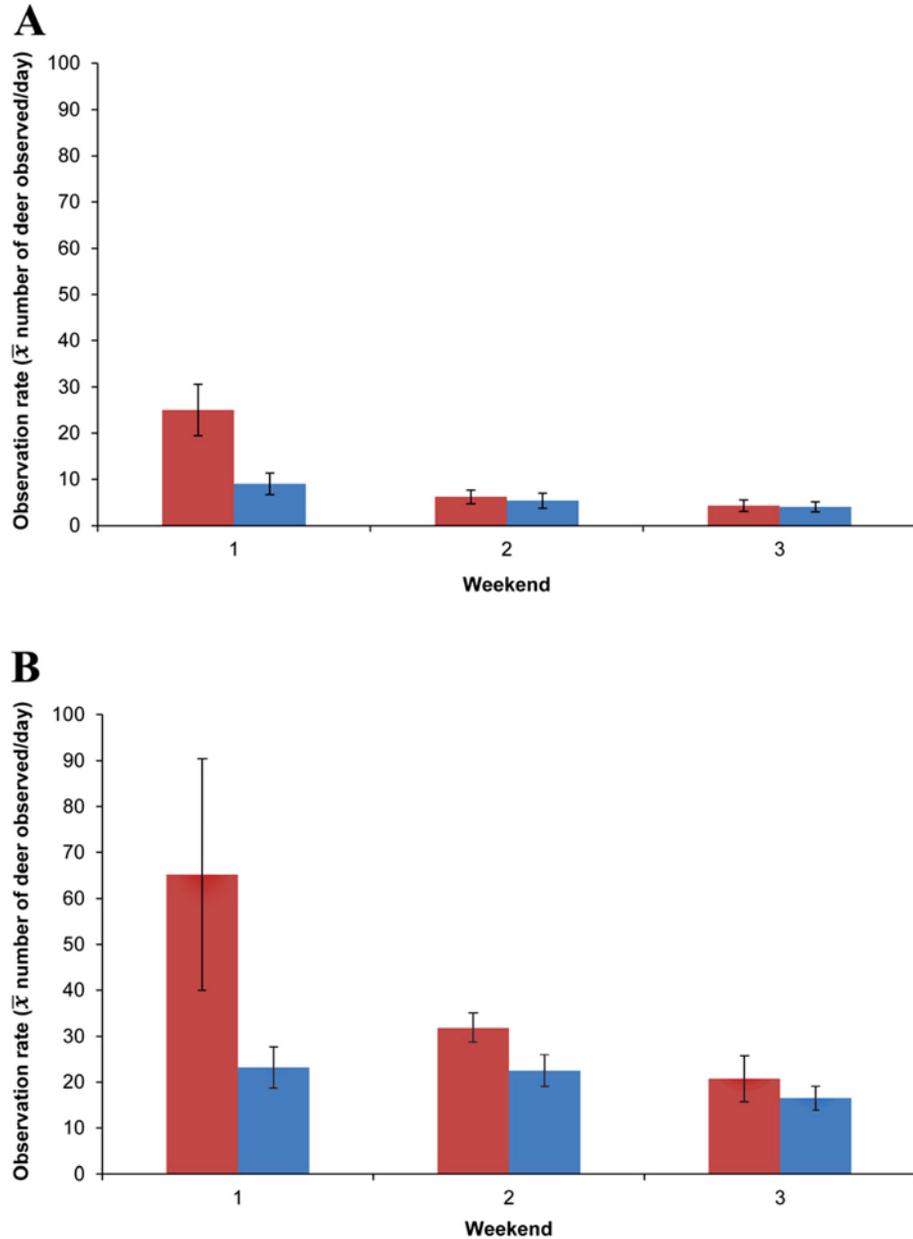
Figure 3. Observation rate ($\bar{x}$ no. of unmarked, antlered [A] and antlerless [B] white-tailed deer [*Odocoileus virginianus*] observed per day) by hunters within the low- (blue bar) and high-risk treatments (red bar) on the Samuel Roberts Noble Foundation Oswalt Ranch located in Love County, Oklahoma, USA, during 3 weekends (1 = 22–23 Nov 2008, 21–22 Nov 2009; 2 = 28–30 Nov 2008, 27–29 Nov 2009; 3 = 6–7 Dec 2008, 5–6 Dec 2009) of the rifle–firearm seasons. Error bars reflect ± 1 standard error of the mean for deer observed per day during each weekend of the hunting season across the low- and high-risk treatments.

treatment declined markedly (both in relative and absolute terms) compared with the low-risk treatment. These results provide further evidence that both antlered and antlerless deer recognize risk posed by hunters and alter their behavior to avoid encounters with hunters. Though a limited number of deer were harvested each year, we do not believe that the level of harvest (2008: n = 12, 1 deer/97.4 ha; 2009: n = 18, 1 deer/70.1 ha) resulted in an appreciable reduction of the total population size. Therefore, declining observation rates over time were not likely biased by harvest, which was distributed over the Oklahoma rifle deer-season.

Movement behavior among individuals was a primary driver in whether a collared deer was susceptible to observation. The greater distance moved, the greater the susceptibility to harvest in the high-risk treatment. Previous research has shown that moving prey (e.g., observed deer) are detected more easily by predators (Lima and Dill 1990). This gives further support to the theory that mobile animals will be observed (Lima and Dill 1990) regardless of the resource types used. Contrary to our hypothesis, we did not observe the same trend in the low-risk treatment; movement rate was similar between observed and unobserved collar deer in the low-risk treatment. This may be an artifact of limited sample size or deer in the low-risk treatment did not recognize the risk as a significant threat. Higher elevation also influenced hunter observations. This may stem from the selection of hunting locations by hunters. Most hunters selected higher elevation locations, which typically provided greater views than lower elevation areas (which primarily consisted of dense riparian vegetation because they occurred along drainages and streams; A. R. Little, personal observation). Although we did not observe an influence of other landscape features (i.e., vegetation type, slope, and distance to nearest road) on probability of observation at temporal scales of <1 hour, it is possible that the broader selection of resources could influence susceptibility to harvest. For example, resource selection of elk at fine temporal scales and in an area with intense human activity was not correlated strongly with survival (Webb et al. 2011*b*). However, resource selection of elk at broader temporal and spatial scales influenced survival of elk (Dzialak et al. 2011*c*).

Overall, this study provides evidence that human predation risk can decrease observability of white-tailed deer during the hunting season, which may stem from broader temporal scale resource selection patterns that were not analyzed in this study. This study also provides evidence that movement behavior influences deer susceptibility to harvest at a finer temporal scale relative to other behaviors (e.g., resource selection). Our findings suggest that biologists and land managers consider the importance of managing human predation risk on game species to achieve their desired management objectives. Additionally, our temporal changes in observation rates can be used to address hunter concerns of overharvest that are based on decreased observation rates of deer.

Management Implications

Recreational hunters are a primary means to control ungulate population abundance. Therefore, recreational hunters can be used to control population size by promoting early season hunting at higher risk levels (e.g., 1 hunter/30 ha) before deer recognize risk across the landscape, at which time deer observability and susceptibility to harvest will decline. Quantifying behavioral characteristics of the most successful hunters and incorporating this information into educational outreach programs may facilitate harvest. However, further analysis of hunter behavior is needed to develop successful hunting practices targeted at increasing harvest. In contrast, reduction of harvest, while maintaining overall hunter participation, can be accomplished through extending hunting seasons and lowering human predation risk because deer likely will not perceive the risk and alter behavior as quickly compared with higher risk levels.

Literature Cited

Abrams, P. A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. Ecology 81:2902– 2913.

Altendorf, K. B., J. W. Laundré, C. A. L. González, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430–439.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools Accessed 1 May 2009.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behavior of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7:e50611.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Collins, C., and R. Kays. 2011. Causes of mortality in North American populations of large and medium-sized mammals. Animal Conservation 14:474–483.

Conover, M. R. 2002. Resolving human–wildlife conflicts: the science of wildlife damage management. Lewis, Boca Raton, Florida, USA.

Creel, S., D. Christianson, S. Liley, and J. A. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960.

Decker, D. J., and L. C. Chase. 1997. Human dimensions of living with wildlife—a management challenge for the 21st century. Wildlife Society Bulletin 25:788–795.

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011*a*. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE 6: e14597.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011*b*. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273.

Dzialak, M. R., S. L. Webb, S. M. Harju, J. B. Winstead, J. Wondzell, J. P. Mudd, and L. D. Hayden-Wing. 2011*c*. The spatial pattern of demographic performance as a component of sustainable landscape management and planning. Landscape Ecology 26:775–790.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, and J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: A critical evaluation of a time-honored technique. Wildlife Society Bulletin 30:387–393.

Gee, K. L., J. H. Holman, and S. Demarais. 1999. A man-power efficient drop-net system for capturing white-tailed deer. 22nd Annual Southeast Deer Study Group Meeting 22:31.

Gee, K. L., M. D. Porter, S. Demarais, and F. C. Bryant. 2011. White-tailed deer: their foods and management in the Cross Timbers. Third edition. Samuel Roberts Noble Foundation Publication NF-WF-11-02, Ardmore, Oklahoma, USA.

Grau, G. A., and B. L. Grau. 1980. Effects of hunting on hunter effort and white-tailed deer behavior. Ohio Journal of Science 80:150–156.

Haines, A. M., D. Elledge, L. K. Wilsing, M. Grabe, M. D. Barske, N. Burke, and S. L. Webb. 2012. Spatially-explicit analysis of poaching activity as a conservation management tool. Wildlife Society Bulletin 36:685–692.

Halls, L. 1973. Managing deer habitat in loblolly–shortleaf pine forest. Journal of Forestry 71:752–757.

Karns, G. R., R. A. Lancia, C. S. DePerno, and M. C. Conner. 2012. Impact of hunting pressure on adult male white-tailed deer behavior. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 66:120–125.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior white-tailed deer: implications for conservation of the Florida panther. Conservation Biology 12:1359–1364.

Kilpatrick, H. J., A. M. LaBonte, and J. T. Seymour. 2002. A shotgun–archery deer hunt in a residential community: evaluation of hunt strategies and effectiveness. Wildlife Society Bulletin 30:478–486.

Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Wildlife Veterinary Services, Laramie, Wyoming, USA.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. Bioscience 54:123–138.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lima, S. L., and T. D. Steury. 2005. Perception of predation risk: the foundation of nonlethal predator–prey interactions. Pages 166–188 *in* P. Barbosa, and I. Castellanos, editors. Ecology of predator–prey interactions. Oxford University Press, New York, New York, USA.

Little, A. R. 2011. Human predation risk effects on adult, male white-tailed deer antipredator behavior. Thesis, Mississippi State University, Mississippi State, USA.

McLoughlin, P. D., J. S. Dunford, and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74:701–707.

Messmer, T. A. 2009. Human–wildlife conflicts: emerging challenges and opportunities. Human–Wildlife Conflicts 3:10–17.

Murphy, D. A. 1965. Effects of various opening days on deer harvest and hunting pressure. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 19:141–146.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533–541.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience 54:755–766.

Root, B. G., E. K. Fritzell, and N. F. Giessman. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin 16:145–151.

Rutledge, D. T., and C. A. Lepczyk. 2002. Landscape change: patterns, effects, and implications of adaptive management of wildlife resources. Pages 312–333 *in* J. Liu, and W. W. Taylor, editors. Integrating landscape ecology into natural resources management. Cambridge University Press, Cambridge, England, United Kingdom.

Sage, R. W. Jr., W. C. Tierson, G. F. Mattfeld, and D. F. Behrend. 1983. White-tailed deer visibility and behavior along forest roads. Journal of Wildlife Management 47:940–953.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63:437–443.

Skogland, T. 1991. What are the effects of predators on large ungulate populations? Oikos 61:401–411.

U.S. Department of Agriculture-Geospatial Data Gateway [USDA-GDG]. 2008. USDA-GDG home page. http://datagateway.nrcs.usda.gov/ Accessed 24 Nov 2008.

U.S. Department of Agriculture-Geospatial Data Gateway [USDA-GDG]. 2010. USDA-GDG home page. http://datagateway.nrcs.usda.gov/ Accessed 27 Apr 2010.

Valeix, M., A. J. Loveridge, S. Chamaille-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30.

Van Etten, R. C., D. F. Switzenberg, and L. Eberhardt. 1965. Controlled deer hunting in a square mile exclosure. Journal of Wildlife Management 29:59–73.

Webb, S. L., M. R. Dzialak, R. G. Osborn, S. M. Harju, J. J. Wondzell, L. D. Hayden-Wing, and J. B. Winstead. 2011*a*. Using pellet groups to assess response of elk and deer to roads and energy development. Wildlife Biology in Practice 7:32–40.

Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011*b*. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. Population Ecology 53:483–493.

Webb, S. L., J. A. Gaskamp, K. L. Gee, S. Demarais, and A. R. Little. 2011*c*. Design of an underwater telemetry antenna for locating and retrieving submerged radio collars. Wildlife Society Bulletin 35:101–104.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Using fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210–1217.