Experimental Evidence of Spatial Memory and Home Range Affinity in White-tailed Deer (*Odocoileus virginianus*)

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The role of spatial memory in the movement of animals through landscapes remains elusive. To examine spatial memory and home range affinity of White-tailed Deer (*Odocoileus virginianus*) in northeastern Minnesota during 1995–2007, I translocated 17 adult does with known home ranges to unfamiliar sites and radio-tracked them after their release. Twelve does wearing transmitting radio-collars returned to their home ranges. Death and collar expiration precluded determination of whether the remaining five does would have returned to home ranges. Three of five does wearing global positioning system collars traveled throughout hundreds of square kilometres, circling, backtracking, and returning to release sites, while two others exhibited directional movement for tens of kilometres. Four does that survived to parturition stopped traveling and moved at hourly rates similar to those of control does during the first three weeks of the typical fawn-rearing period, but continued traveling later. Their aberrant extensive travel before and after interruption by parturition suggests that they recognized they were in unfamiliar areas, demonstrating both their capacity and propensity to search for and occupy the familiar space of their individual home ranges. Their successful return to home ranges provided experimental evidence of spatial memory and further elucidated its pervasive role in White-tailed Deer spatial ecology.

Key Words: experimental translocation; home range; movements; *Odocoileus virginianus*; spatial affinity; spatial memory; White-tailed Deer

Introduction

The role of spatial memory in how animals move through landscapes remains elusive and its quantification challenging (Moorcroft 2012; Spencer 2012; Fagan *et al.* 2013). Memory effects in the spatial ecology of animals were postulated in the earliest observations of the movements of individual animals and were eventually confirmed with the development of radio-tracking technology (M]oorcroft 2012). With parallel advances in cognitive sciences and statistical analyses of animal movements, the influence of spatial memory is increasingly being recognized and incorporated into mathematical models of animal movement (Gautestad and Mysterud 2005; Borger *et al.* 2008; Gautestad 2011; Moorcroft 2012; Spencer 2012; Gautestad *et al.* 2013).

Because spatial memory is an internal cognitive process, movements based on memory may be directed toward space beyond an animal's current field of perception (Gautestad and Mysterud 2005; Moorcroft 2012; Fagan *et al.* 2013). Thus, to distinguish memory-based movements from movements elicited by the immediate external environment requires experimental manipulation (Moorcroft 2012). However, the spatial memory that animals possess before experimentation begins is unknown to researchers. Fagen *et al.* (2013)

suggest one solution to this problem is tracking the spatial dynamics of juveniles throughout ontogeny to obtain complete movement histories before experimentation. They further suggest translocating these animals to novel environments, which may help identify movements influenced by previous spatial memories.

The movements of adult female White-tailed Deer (*Odocoileus virginianus*) and their fawns in northeastern Minnesota indicated that spatial memories developed by fawns following their mothers was a primary influence on their adult home-range locations, seasonal migrations, and landscape distribution (Nelson and Mech 1981, 1987, 1999, 2006; Nelson 1994, 1998). Further evidence of spatial memory was inferred from a pilot study in which adult females and fawns were translocated to unfamiliar areas (Nelson 1994). Some deer returned to their home ranges and resumed their previous movement patterns, while others did not return, but mimicked their pre-translocation movements near their release sites.

Traditional movements and home-range affinity not only suggest the capacity for spatial memory, but also imply a fitness advantage of the propensity to occupy familiar space. To collect experimental evidence of this capacity and propensity, I delineated the home ranges

of adult does for at least a year before translocating them outside their home ranges. I then examined their movements relative to their home ranges and to the movements of does not translocated. If spatial memory was a major factor responsible for home range affinity, then translocated does would be predicted to return to their home ranges and not remain at their release sites or other sites they encountered that supported resident deer. A corollary of this prediction is that translocated does would employ different modes of movement than those of control does not translocated.

Study Area

I conducted this study in the Superior National Forest in northeastern Minnesota (48°N, 91°W). The topography was flat, and the area was dominated by lakes and mixed coniferous–deciduous forests (Heinselman 1996). Average monthly minimum temperatures ranged from 2°C to 18°C from May to October and −18°C to 7°C from November to April (Heinselman 1996). Snow cover generally occurred from November through April with weekly depths averaging 31–64 cm during February and March and 0–30 cm during April (Nelson and Mech 2006).

Most deer in the study area migrated from one of two winter concentration areas, roughly 30 km^2 each, and averaged 12-km and 25-km migrations to reach individual summer ranges, some up to 80 km distant (Nelson and Mech 1987). Deer migrated to summer ranges during late March and early April when summer range density was 1–3 deer/km^2 (Lenarz 2002). Parturition occurred primarily during the last week of May and first week of June (Kunkel and Mech 1994). Deer occupied 0.7–1.0 km^2 summer ranges (Nelson and Mech 1981) before returning to the winter concentrations during November to January, where densities were over 15 deer/km^2 (Nelson and Mech 1987). Gray Wolf (*Canis lupus*) predation and human hunting were the main causes of deer mortality (Nelson and Mech 1986). Wolves along with Black Bears (*Ursus americanus*) were major predators of newborn fawns during their first weeks of life (Kunkel and Mech 1994).

Methods

I captured adult does during February-April when they occupied winter concentration areas (Nelson and Mech 1981). I anesthetized them (Kreeger 1996), extracted an incisor for aging (Nelson 2001), and fitted them with very high frequency (VHF) radio collars or Global Positioning System (GPS) collars (Merrill *et al.* 1998). I radio-tracked VHF-collared does from the air two to four times weekly. GPS-collared does yielded locations every hour, which I downloaded to a spreadsheet after remotely releasing the collars (Mech and Gese 1992) or retrieving them after mortality occurred.

I subsequently recaptured, recollared, and translocated while sedated, those adult does radio-tracked a

minimum of 1 year. I translocated them 10-25 km outside their home ranges to unfamiliar (no previous radio-locations) and familiar (previous radio locations) release sites. I separated the two groups when describing and analyzing their movements. I recorded the number of days they used to return to their home ranges, or if not returning, the number of days radio-tracked until they died or their radio-collars expired.

I used data from both VHF- and GPS-collared does to measure propensity to return to home ranges after being translocated, but only data from GPS-collared does to describe and quantify movements. To provide experimental controls for comparing with translocated GPS-collared does rearing fawns, I captured and released does at their capture sites wearing GPS collars programmed to record hourly locations starting 16 May, 1 week before parturition and continuing through the first 3 weeks of fawn rearing to 23 June.

I measured area used by GPS-collared does by calculating minimum convex polygons (MCP) of their locations (Mohr 1947). I differentiated two modes of movement: directional travel and all other movement based on rate (m/h) measured by distance between hourly locations. I identified and defined travel based on migrating GPS-collared deer traveling 1.5 km/h (SD = 0.6, n = 27, Nelson *et al.* 2004). Because 95% of their hourlymigration travel exceeded 300 m/h and was sustained for 3–6 h per travel periods (Nelson *et al.* 2004), I classified as "travel" in this study, directional movement of > 300 m during each of at least 3 sequential hours. These criteria separated directional travel from all other movements, including those that slowed, circled, or deviated from directional movement.

I contrasted movement behaviours and MCPs of translocated GPS-collared does with those of control GPS-collared does and further compared their hourly movement rates during each week starting 16–23 May and during the first 3 weeks of the fawn-rearing period. I assumed the timing of parturition based on a pattern of spatially constricted locations by parturient does (Kunkel and Mech 1994). This sampling corresponded to the following biological ontogeny: a period before fawns are born; the first week of fawn rearing, which requires maternal care and defensive behaviour by the doe and suckling and hiding behaviour of fawns; the second week of fawn rearing, when the transition from hiding to running begins as a response by fawns to danger (Jackson *et al.* 1972); the third week of fawn rearing, when fawns generally run from danger.

I analyzed hourly movement rates by estimating means and 95% confidence limits (Cherry 1998; Anderson *et al.* 2001; Johnson 2002). I further compared hourly movement rates of translocated does with those of control does during each week sampled in the pre-fawn and fawn-rearing periods, by using *t*-tests and accepting statistical significance at $P < 0.05$ and when 95% CLs on the mean differences did not include zero.

I followed the American Society of Mammalogists' guidelines (Sikes and Gannon 2011) and the Animal Care and Use Committee study plan 2700202, Patuxent Wildlife Research Center, United States Fish and Wildlife Service.

Results

I captured and radio-collared 26, 1–13 year-old does (median = 6 years old) during February-April 1995–2007. Of the 26 does, I radio-tracked 17 for 1–4 years (median = 2 years) before recapturing and translocating them 10-25 km (median = 13 km) outside their current home ranges. I captured two of them a third time and translocated them to familiar sites that they previously occupied but located outside their current home ranges. I released the remaining nine does at their capture sites to serve as experimental controls for hourly movement comparisons to translocated does during the fawn rearing period.

Radio-tracking of translocated does yielded 2–111 (median = 46) locations from 12 VHF-collared does and 709–4150 (median = 2605) locations from seven GPS-collared does, acquiring 58–95% (median = 84%) of potential locations. Nine control GPS-collared does yielded 341–655 (median = 453) locations, 36–70% (median = 50%) of potential locations.

Return to home ranges

Twelve of 17 (71%) does that were translocated to unfamiliar sites returned to their home ranges. Ten returned within 1–89 days (median = 22 days) and the other two returned 1.3 and 3.2 years later. The remaining five does failed to return to home ranges as three died and the collars on two others expired (80–275 days, median 174 days). The two does translocated to familiar sites outside their current home ranges also returned to their home ranges.

GPS-collared does released at unfamiliar sites

From March through September 2004 through 2006, five translocated GPS-collared does released at unfamiliar sites traveled directionally, circled, backtracked, and returned to or toward their release sites (Table 1, Figure 1). Does 8164, 8180, and 8252 roamed extensively and the other two (7958 and 8172) traveled directly. Doe 7958 moved directly to her adult summer range to which she had dispersed 3 years earlier as a 1 year old. The bearings and distances for her dispersal movements include the region of her release site, although she was never located there. Doe 8172 moved in a direction away from her home range before backtracking 76% of the distance to her release site (Table 1). Hourly movement rates combined comprised 4% travel and 96% nontravel movement (Table 1). The does moved ten times faster when traveling than at other times (877 m/h vs. 83 m/h, respectively, Table 1).

GPS-collared does released at familiar sites

In late March and early April, I translocated GPS-collared does 7904 and 7940 to familiar sites: 7904 to

TABLE 1. Rates and patterns of travel and nontravel movement* of translocated GPS-collared adult female White-tailed Deer (*Odocoileus virginianus*) in northeastern Minnesota, March-September, 2004-2007.

Doe	Travel period	Travel rate Mean, m/h	95% CL	n	Nontravel rate Mean, m/h	95% CL	n	Movement pattern MCP, km²	Direct travel, km	No. of locations
Released at unfamiliar site										
7958	1–30 Mar	NA	NA	NA	54	9	521	NA	22	588
8164	22 Mar – 7 Sep	840	151	28	56	4	1859	595	NA	2367
8172	9 Apr – 30 Sep	1118	355	19	90	7	2083	NA	42	808
8180	22 Mar – 21 Sep	893	57	243	96	6	3707	309	NA	4140
8252	2 Apr – 7 Jul	803	96	96	83	6	1939	180	NA	2128
Combined	—	877	48	386	83	3	10109	NA	NA	NA
Released at familiar site										
7904	28 Mar – 16 Apr	881	170	28	85	17	394	143	NA	435
7940	1–9 Apr	1064	513	5	56	15	72	NA	22	109
Combined	—	909	155	33	85	14	465	NA	NA	544

Note: CL = confidence limits, MCP = minimum convex polygon, NA = Not applicable
*Travel is directional movement of > 300 m during each of at least 3 sequential hours; nontravel is all other movements, including those that slowed, circled, or deviated from directional movement.
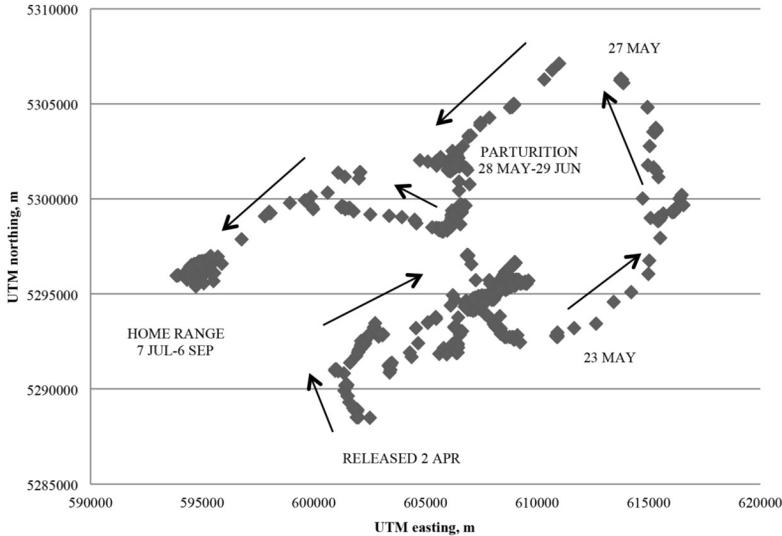
FIGURE 1. The 3510 hourly locations recorded for GPS-collared White-tailed Deer (*Odocoileus virginianus*) doe 8252 from 2 April, when she was released at an unfamiliar site 10 km from her home range, to 6 September 2006 in northeastern Minnesota. Arrows depict her general direction of travel starting at the release site and arriving at her home range on 7 July.

a previous release site that she had used 7 years earlier and 7940 to her natal home range from which she had dispersed 5 years earlier as a 1 year old.

Doe 7904 traveled extensively, circling and back-tracking for 19 days before reaching her winter home range (Table 1). She remained there 15 h before migrating directly to her summer range. Doe 7940 traveled directly for 22 km, including 4 km of backtracking to reach her winter range in 8 days (Figure 2). She remained there 8 days before migrating 11 km to her summer range. Their combined hourly movement rates comprised 7% travel and 93% nontravel movement (Table 1). They moved ten times faster when traveling than at other times (909 m/h vs. 85 m/h, Table 1).

GPS-collared does during fawn rearing

Translocated GPS-collared does 8164, 8172, 8180, and 8252 stopped their extensive travel in mid-May before parturition, which began for them and nine control GPS-collared does between 25 May and 6 June (median = 31 May). During 12–28 (median = 23) sequential days of fawn rearing, both groups occupied 0.2–1.3 km^2 (median = 0.5 km^2).

Translocated and control does moved at the same mean hourly rates during 7 days in mid-May before fawn rearing and also during the first week of fawn rearing (Table 2). Control does moved faster than translocated does during the second week of fawn rearing, but not in the third week (Table 2). Translocated does permanently departed their fawn rearing areas after

TABLE 2. Rate of movement of translocated and control GPS-collared adult female White-tailed Deer (*Odocoileus virginianus*) in northeastern Minnesota a week before parturition (16–23 May 2001-2006) and during three weeks after parturition while rearing fawns.

Period	Translocated does			Control does		
	Mean, m/h	95% CL	*n*	Mean, m/h	95% CL	*n*
Preparturition (1 week)	79	9	586	88	8	639
Fawn rearing						
First week	66	6	524	74	6	707
Second week	83*	9	475	109*	9	598
Third week	97	13	356	105	8	643

Note: CL = confidence limits.
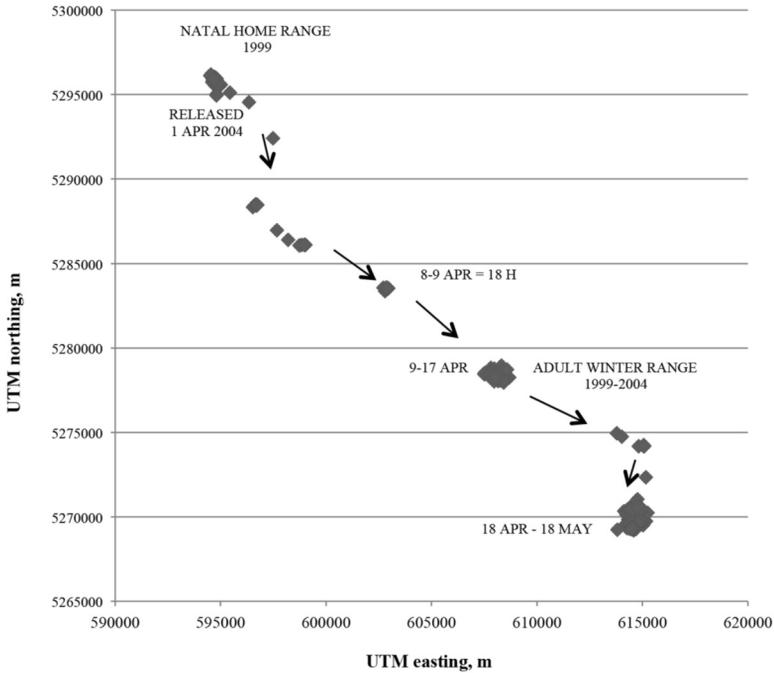*Significant difference between translocated and control does (*p* < 0.005, *t* test).

FIGURE 2. The 710 hourly locations, recorded between 1 April and 18 May 2004, for GPS-collared White-tailed Deer (*Odocoileus virginianus*) doe 7940 captured on her winter range and translocated 22 km to a familiar site (her natal home range) 5 years after natal dispersal. Arrows depict her general direction of travel starting at her release site, traveling 22 km, arriving on her adult winter home range on 9 April, subsequently traveling 11 km further to her adult summer home range, and arriving on 18 April.

12–45 days (median = 26 days) and continued traveling, while control does remained on their home ranges.

Discussion

All translocated does left their release sites, which had resident deer present, suggesting that the resources for deer survival were present. Thus, lack of habitat appeared an unlikely factor influencing their departure. Aggression by resident deer toward the translocated does can also be excluded as a factor, as elsewhere in the study area, sympatric wintering deer moved independently of each other, suggesting that competition for space was not influencing their movements (Nelson and Sargeant 2008). Similarly, Jones *et al.* (1997) observed no effect on movement of resident deer from the presence of translocated deer. Although conflict is observed at artificial feeding sites, which attract large numbers of deer, such disputes appear restricted to feeding behaviour (Ozoga 1972).

There was large variation in the amount of time taken to return to home ranges despite the fact that 87% of the does were translocated similar distances (13–15 km). I previously found that female yearlings made 7–22-km forays beyond their natal ranges (Nelson 1998), and some dispersed 18–168 km to new home ranges (Nelson 1993). Thus, spatial memories estab-

lished during exploratory or dispersal movements could have been one factor influencing variation in return time over similar distances. Conceivably, some does encountered areas they recognized from previous exploratory or dispersal movements and then navigated accordingly to return to familiar space. Others not encountering familiar areas would necessarily spend more time roaming if spatial memory was the primary mechanism they used as they attempted to return to home ranges.

The movements of four of five GPS-collared does translocated to unfamiliar release sites suggest that they were looking for familiar space. Their extensive travel far exceeded that necessary to acquire the resources for daily survival evinced by adult does in the study area that were occupying home ranges < 1% the size of spaces traveled by translocated does (Nelson and Mech 1981). Their movements further suggest that translocated does simultaneously developed new spatial memories, evidenced by backtracking and returning to release sites.

The direct travel to her home range by the fifth GPS-collared doe suggests that the release site was part of the spatial memory she had developed during natal dispersal movements in the region of the release site as she established her adult home range. Direct travel

by the two GPS-collared does released on familiar sites after being absent from them 5 and 7 years also indicates that they recognized their surroundings, although only one traveled like deer migrating annually between summer and winter home ranges (Nelson *et al.* 2004). The additional roaming, circling, and backtracking of the other doe hints at variation in the longevity of spatial memory and highlights the challenge of understanding and including it in models of animal movement.

The movements of the one doe translocated to an unfamiliar release site, traveling directly and backtracking toward her release site, contrasts sharply with her roaming cohorts. Given the small sample size and the fact that she was nonmigratory before being translocated, it is difficult to interpret her movements. She may have been behaving similar to three translocated deer that appeared to invoke memory of their previous migration pattern (Nelson 1994). Migrating Siberian roe deer (*Capreolus pygarus*), captured and translocated to unfamiliar areas while migrating, mimicked the same migration direction and distances as their cohorts (Danilkin *et al.* 1994). These examples suggest that at least two cognitive processes operate to achieve spatial orientation: one depending on memory of bearing and distance patterns to direct movement, and another involving roaming and searching for familiar space to determine direction of travel.

When translocated GPS-collared does stopped traveling just before parturition, they moved at the same hourly rates as control GPS-collared does and, subsequently, constricted their movements, as did control does, indicating that both groups gave birth and cared for their fawns (Nelson and Mech 1981; Ozoga *et al.* 1982; Kunkel and Mech 1994). The similar movement rates of both groups during the first week of fawn rearing suggest that translocated does may not have experienced any negative behavioural or physiological effects from their extensive travel before parturition. The increased rate of movement by control does, compared with translocated does, in the second week of fawn raising suggests possible differences as fawns matured. However, in the subsequent week, both groups moved at the same rate indicating an overall pattern of similar movement rates before and while rearing fawns.

The duration of restricted movement of does after giving birth further indicates that they nurtured their fawns beyond the period of fawn concealment and inactivity, well into the period when fawns regularly follow their mothers (Jackson *et al.* 1972). This further indicates adequacy of nutrition for maintenance as well as that needed to sustain lactation. I do not know if the fawns survived and followed their mothers when they continued roaming. Regardless, the relevant and overriding result is that the biological imperative of parturition and fawn rearing took temporary precedence over travel for the translocated does. This is a clear example of changes in movements determined by opposing internal processes: one directing parturition and nurturing behaviour and the other emanating from the capacity for spatial cognition and the propensity to occupy familiar space.

All translocated does left their release sites, and those surviving with transmitting radio-collars returned to their home ranges. The translocated GPS-collared does did this despite having met their nutritional and physiological demands while traveling through hundreds of square kilometres, three orders of magnitude larger than home ranges of adult does. Thus they moved continually beyond daily field of perception to eventually arrive at the exact site they occupied before being translocated. This clearly demonstrates not only the capacity for spatial memory, but also the propensity to return to familiar space. The extremely aberrant roaming of the GPS-collared does can only be understood as searching the landscape for space that was remembered and recognized when finally found.

The dominant paradigm of ungulate movement is based on the premise that movement is directed by innate optimal foraging in the field of perception. Mathematical modeling has accepted this premise, ignoring behavioural mechanisms, such as the influence of spatial memory (Gautestad and Mysterud 2005). However, it has become increasingly clear that spatial memory plays an integral role in animal movement and must be included in models to achieve biological reality in predicting movements. Fagan *et al.* (2013) recognized this as part of an "emerging research interface" of behavioural ecology, cognitive science, animal tracking, and quantitative ecology. The findings herein contribute to their call for experimental evidence of spatial memory and further elucidate its pervasive role in the spatial ecology of White-tailed Deer.

Acknowledgements

Literature Cited

Anderson, D. R., W. A. Link, D. H. Johnson, and **K. P. Burnham.** 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Management 65: 373–378.

Börger, L., B. D. Dalziel, and **J. M. Fryxell.** 2008. Are there general mechanisms of animal home-range behaviour? A review and prospects for future research. Ecology Letters 11: 637–650.

Cherry, S. 1998. Statistical tests in publications of The Wildlife Society. Wildlife Society Bulletin 26: 947–953.

Fagan, W. F., M. A. Lewis, M. Auger-Methe, T. Avgar, S. Benhamou, G. Breed, L. LaDage, U. E. Schlagel, W. Tang, Y. P. Papastamatiou, J. Forester, and **T. Mueller.** 2013. Spatial memory and animal movement. Ecology Letters 16: 1316–1329.

Danilkin, A. A., Y. A. Darman, and **A. N. Minaev.** 1994. Homing by migratory Siberian deer. Doklady Biological Sciences 332 5: 358–360.

Gautestad, A. O. 2011. Memory matters: influence from a cognitive map on animal space use. Journal of Theoretical Biology 287: 26–36.

Gautestad, A. O., and **I. Mysterud.** 2005. Intrinsic scaling complexity in animal dispersal and abundance. American Naturalist 165:44–55.

Gautestad, A. O., L. E. Loe, and **A. Mysterud.** 2013. Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer *Cervus elaphus* movements with simulation models. Journal of Animal Ecology 82: 572–586.

Heinselman, M. L. 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis, Minnesota, USA.

Jackson, R. M., M. White, and **F. F. Knowlton.** 1972. Activity patterns of young white-tailed deer fawns in south Texas. Ecology 53: 262–270.

Johnson, D. H. 2002. The role of hypothesis testing in wildlife science. Journal of Wildlife Management 66: 272–276.

Jones, M. L., N. E. Mathews, and **W. F. Porter.** 1997. Influence of social organization on dispersal and survival of translocated female white-tailed deer. Wildlife Society Bulletin 25: 272–278.

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

Kunkel, K. E., and **L. D. Mech.** 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72: 1557–1565.

Lenarz, M. S. 2002. White-tailed Deer of Minnesota's Forested Zone: Harvest, Population Trends, and Modeling 2003. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Mech, L. D., and **E. M. Gese.** 1992. Field testing the Wildlink capture collar on wolves. Wildlife Society Bulletin 20: 249–256.

Merrill, S. B., L. G. Adams, M. E. Nelson, and **L. D. Mech.** 1998. Testing releasable GPS radiocollars on wolves and white-tailed deer. Wildlife Society Bulletin 26: 830–895.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223–249.

Moorcroft, P. R. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. Journal of Mammalogy 93: 903–916.

Nelson, M. E. 1993. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. Journal of Mammalogy 74: 316–322.

Nelson, M. E. 1994. Migration bearing and distance memory by translocated White-tailed Deer, *Odocoileus virginianus.* Canadian Field-Naturalist 108: 74–76.

Nelson, M. E. 1998. Development of migratory behavior in northern white-tailed deer. Canadian Journal of Zoology 76: 426–432.

Nelson, M. E. 2001. Tooth extractions from live-captured white-tailed deer. Wildlife Society Bulletin 29: 245–247.

Nelson, M. E., and **L. D. Mech.** 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 77: 1–53.

Nelson, M.E., and **L. D. Mech.** 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 50: 691–698.

Nelson, M. E., and **L. D. Mech.** 1987. Demes within a northeastern Minnesota deer population. Pages 27–40 *in* Mammalian Dispersal Patterns. *Edited by* B. D. Chepko-Sade and Z. Halpin. University of Chicago Press, Chicago, Illinois, USA.

Nelson, M. E., and **L. D. Mech.** 1999. Twenty-year home-range dynamics of a white-tailed deer matriline. Canadian Journal of Zoology 77: 1128–1135.

Nelson, M. E., and **L. D. Mech.** 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. American Midland Naturalist 155: 373–382.

Nelson, M. E., L. D. Mech, and **P. F. Frame.** 2004. Tracking of white-tailed deer migration by Global Positioning System. Journal of Mammalogy 85: 505–510.

Nelson, M. E., and **G. A. Sargeant.** 2008. Spatial interactions of yarded White-tailed Deer, *Odocoileus virginianus.* Canadian Field-Naturalist 122: 221–225.

Ozoga, J. J. 1972. Aggressive behavior of white-tailed deer at winter cuttings. Journal of Wildlife Management 36: 861–868.

Ozoga, J. J., L. J. Verme, and **C. S. Bienz.** 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. Journal of Wildlife Management 46: 1–11.

Sikes, R. S., and **W. L. Gannon.** 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92: 235–253.

Spencer, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93: 929–947.