

# TRACKING OF WHITE-TAILED DEER MIGRATION BY GLOBAL POSITIONING SYSTEM

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We used global positioning system (GPS) radiocollars on female white-tailed deer (*Odocoileus virginianus*) to document details of onsets of migrations, rates of travel, patterns of travel, durations of migrations, and distances traveled by 8 deer in spring and 4 deer in autumn in northeastern Minnesota in 1998, 1999, and 2001. In spring, deer migrated 23–45 km during 31–356 h, deviating a maximum 1.6–4.0 km perpendicular from a straight line of travel between their seasonal ranges. They migrated a minimum of 2.1–18.6 km/day over 11–56 h during 2–14 periods of travel. Minimum travel during 1-h intervals averaged 1.5 km/h ( $SD = 0.6$ ,  $n = 27$ ). Deer paused 1–12 times, averaging 24 h/pause ( $SD = 29$ ,  $n = 43$ , range 19–306 h/pause). Deer migrated similar distances in autumn with comparable rates and patterns of travel. A difference of 1.9- to 7.5-fold in duration of migrations by deer migrating the same distances suggests that much of the variation in durations may be independent of migration distance.

Key words: deer, GPS tracking, migration, movements, *Odocoileus virginianus*, radiotracking, travel

Early research documented white-tailed deer (*Odocoileus virginianus*) migration by recovering ear tags from deer marked on winter ranges and killed during autumn hunting (Carlsen and Farnes 1957; Olson 1938; Verme 1973). With radiotelemetry, knowledge about timing, duration, and route of migration became possible. Using automated radiotracking (Cochran et al. 1965), Rongstad and Tester (1969) documented migration travel every 10–15 min before radiocollared deer migrated beyond the short receiving range (3 km). Subsequent studies using portable tracking systems documented complete migrations elsewhere, but locations were obtained only daily or weekly because of time, logistical, and personnel constraints typical of standard radiotelemetry methods (Drolet 1976; Nelson and Mech 1981; Sabine et al. 2002; Tierson et al. 1985; Van Deelen et al. 1998). Thus, many details, such as onsets of migration, rates of travel, and travel patterns while migrating, were not determined. For example, pausing or

lingering during migration appeared related to temperature (Nelson and Mech 1981), but its frequency was unknown. Moreover, detailed knowledge of migration and differences among individuals could enhance our understanding of the energetics of deer migration and what role migration or energetics plays in the reproductive success of individuals and thus in the productivity of migratory deer populations. Additionally, fine-scale details of migration could contribute insight to understanding security aspects of migration because it takes deer through unfamiliar terrain where they may be most vulnerable to predation.

With development of releasable global positioning system (GPS) collars for medium-size mammals (Merrill et al. 1998), most barriers to detailed study of deer migration were removed. We used GPS radiocollars to document dates and times of migration onsets, distances migrated, durations of migrations, daily rates of migration, 1-h rates of travel, and patterns of travel.

## MATERIALS AND METHODS

The deer we studied wintered in the Garden Lake Deeryard in northwestern Lake County, Minnesota (48°N, 91°W), and summered to the north and east within the Boundary Waters Canoe Area

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TABLE 1.—Migration statistics for GPS-collared female white-tailed deer in northeastern Minnesota, 1998–1999, and 2001.

Deer no.	Year and season	Weight (kg)	Age (years)	Travel						
				Total travel		Daily migration rate (km/day)	Periods		Pauses	
				Distance (km)	Duration (h)		<i>n</i>	Time (h)	<i>n</i>	Time (h)
7840	1999, spring	68	4.9	23	31	17.8	3	11	2	20
7882	1998, spring	61	3.9	25	231	2.6	7	19	6	212
7888	1998, spring	35	0.9	33	52	15.2	6	23	5	29
7920	1999, spring	74	8.9	24	31	18.6	2	12	1	19
7922	1999, spring	65	4.9	45	325	3.3	14	56	12	269
7924	1999, spring	70	10.9	25	92	6.5	3	16	2	76
7928	1999, spring	55	1.9	31	356	2.1	12	50	11	306
7948	1999, spring	65	13.9	31	97	7.7	5	15	4	82
7858	1998, autumn	60	1.6	20	22	21.8	3	14	2	8
7898	1998, autumn	66	11.6	24	17	33.9	2	12	1	5
7956	1999, autumn	70	2.6	22	30	17.6	2	13	1	17
8002	2001, autumn	50	1.6	23	658	0.8	4	19	3	639

Wilderness Area (Nelson 1995; Nelson and Mech 1981). Topography is flat, glaciated Canadian Shield dominated by lakes and rivers (Heinselman 1996). Forests are various mixtures of aspen (*Populus tremuloides*), jackpine (*Pinus banksiana*), and spruce (*Picea*) (Heinselman 1996). Winter temperatures (<0°C) and snow depths of 12–52 cm generally occur from November through April.

After capture in Clover traps (Nelson and Mech 1981), we fitted deer with releasable GPS radiocollars (Merrill et al. 1998) programmed to obtain 1 location per hour except for 1 collar programmed at 1 location per 15 min. Positional accuracy of these collars was generally <100 m with an error polygon <4 ha (Bowman et al. 2000). We electronically released the collars (Mech and Gese 1992) from the deer after migration between seasonal ranges and downloaded location data from collars to a desktop computer for analysis with ArcView GIS software (Environmental Systems Research Institute Inc., Redlands, California).

We defined the onset of migration as travel away from a seasonal range with no return that season. We classified deer movements during migration as either travel or pausing. Pausing was identified as temporary stopping of travel  $\geq 1$  h followed by additional travel. Periods of travel were defined as travel to the 1st pause after leaving a seasonal range, travel between pauses, and travel from the last pause used before entering a seasonal range. Migration distance was measured as the sum of the distances between travel locations while migrating. The duration of the migration period extended from the start of migration to the 1st location when the deer stopped migrating that season. We described the deviation from linear travel by measuring the maximum distance deer traveled perpendicular to a straight line between their winter and summer ranges. We calculated daily rate of migration by dividing the distance of migration by the duration of migration. Rate of travel during 1-h intervals was estimated by measuring the distance between locations 1 h apart in travel time that were preceded and followed by direct travel. We further calculated a crude hourly rate of travel that included all 1-h travel intervals, including those preceded or followed by pauses or seasonal range occupancy. We calculated sizes of pause sites by measuring the area of minimum convex polygons (Mohr 1947) delineated by >10 locations. We presented data for individual deer and analyzed spring and autumn migrations separately. We compared hourly rate of travel based on hourly and 15-min locations from the collar programmed for 1 location/15 min. We referred to individual deer by their ear-tag numbers so they could be identified if used in our other publications.

We used descriptive statistics to examine and present our data (Anderson et al. 2001). We calculated means and *SD* for all deer combined to estimate central tendency for travel time in h/period, hourly rate of travel (hereafter 1-h rate), and time paused (h/pause). Because of our small sample, we used medians and ranges for h/period and h/pause during autumn. We report mean and median distances to the nearest 0.1 km, distances of individual deer to the nearest 1 km, and time intervals to the nearest h.

## RESULTS

We captured 8 adult deer, 3 yearlings, and 1 female fawn during December and March 1998–1999 and 2001 to provide detailed data on spring (8 deer) and autumn (4 deer) migration (Table 1, Figs. 1 and 2). We deployed collars for 13–62 days and recorded 558–1,248 GPS locations per deer. Success rate of programmed location attempts was 63–99%. Approximately 10% of locations were recorded during migration and 90% on summer and winter ranges.

*Spring migration.*—Deer migrated between 4 and 13 April 1998–1999 when snow depths decreased to <9 cm. Median onset time was 1408 h (1200–2000 h), with 7 of 8 onsets in the 7 h before sunset (1900 h). Periods of travel averaged 4 h (*SD* = 2, *n* = 52). As deer traveled, they deviated maxima of 1.6–4.0 km (median = 3.0, *n* = 7) perpendicular from a straight line between seasonal ranges. Travel occurred 70% of the time between 1200 h and sunset (1900 h). Mean minimum 1-h rate of travel was 1.5 km/h (*SD* = 0.6, *n* = 27). Crude hourly rates averaged 1.2 km/h (*SD* = 0.7, *n* = 86).

Pauses averaged 24 h (*SD* = 29, *n* = 43). Eighty-three percent (*n* = 36) of pauses were <24 h duration (*n* = 351 h), but the 16% >24 h (*n* = 499 h) accounted for 60% of the total time deer paused. For pauses lasting <24 h, 52% of time paused occurred between sunset (1900 h) and sunrise (0530 h), 34% between sunrise and 1200 h, and 14% between 1200 h and sunset. Deer paused at sites averaging 0.19 km<sup>2</sup> in area (*SD* = 0.27, *n* = 32,  $\bar{X}$  28 locations per area). Deer 7840 and 7924 migrated separately to sympatric summer ranges but 1st paused in the same area at the same time. They next paused 1 km apart from each other at their 2nd pauses, which were located 6 km

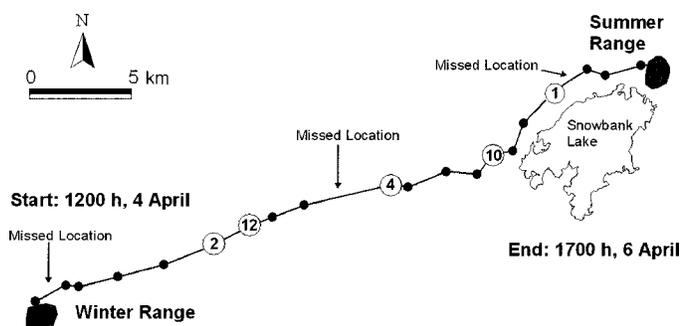


FIG. 1.—Example of a seasonal migration by 1 of 12 white-tailed deer radiotracked with a global positioning system collar in the Superior National Forest of northeastern Minnesota: spring migration of female deer 7888 from winter range to summer range in 1998. Each point represents a location recorded each h. Circles represent pauses, and numbers represent time paused (h). The missed locations result in a 2-h interval between locations.

from their summer ranges. Deer 7840 remained at her 2nd pause site 3 h, while Deer 7924 remained at hers for 61 h before completing her migration.

Unlike their cohorts, 3 deer paused at the onset of their migrations. Deer 7922 paused 7 times (1–62 h) within a distance of 4 km after traveling 4 km from the winter range in 6 h. Her crude hourly rates of travel for that period ( $n = 4$ ) varied between 0.8 and 1.3 km/h. Deer 7948 paused 3 times (18–24 h) within a 4-km linear distance after migrating 3 km from her winter range. Her crude hourly rates of travel between those pauses were 0.5 and 0.9 km/h. Deer 7928 paused 19 h after traveling 2 km from her winter range in 2 h. Her crude hourly rate of travel averaged 0.6 km/h ( $SD = 0.3$ ,  $n = 31$ ) compared to an average of 1.5 km/h ( $SD = 0.6$ ,  $n = 55$ ) by her cohorts. She traveled  $>1$  km/h only 13% of the time (4 of 31 hour intervals), while her cohorts traveled that fast 85% (47 of 55 hour intervals) of the time.

Two deer (7882 and 7922) slowed and reversed their travel during the last half of their migrations. Deer 7882 stopped 4 km short of her summer range for 8.5 days after migrating 16 km in 8 h. She then reversed her direction, traveling 4 km before again reversing and finishing her migration. Deer 7922 migrated 45 km to her summer range and stayed there 5.0 days before returning 15 km to a previous pause site. She remained there for 4.5 days before returning to her summer range.

**Autumn migration.**—Deer started migrating on 29 November 2001, 25 December 1998, 28 December 1999, and 15 January 1999 when snow depths were 9, 15, 15, and 24 cm, respectively. Three deer started between 0800 h and 1000 h and 1 at 1500 h. Periods of travel lasted a median time of 6 h (range 2–8,  $n = 11$ ). Deer deviated maxima of 1.2–2.5 km (median = 1.8,  $n = 7$ ) perpendicular from a straight line of travel between seasonal ranges. Seventy-one percent of the travel occurred between sunrise (0800 h) and sunset (1645 h). Mean 1-h rate of travel was 1.8 km/h ( $SD = 0.4$ ,  $n = 20$ ). Crude hourly rates averaged 1.7 km/h ( $SD = 0.5$ ,  $n = 20$ ). Deer 7956, wearing the collar programmed for 15-min locations, traveled 1.6 km/h

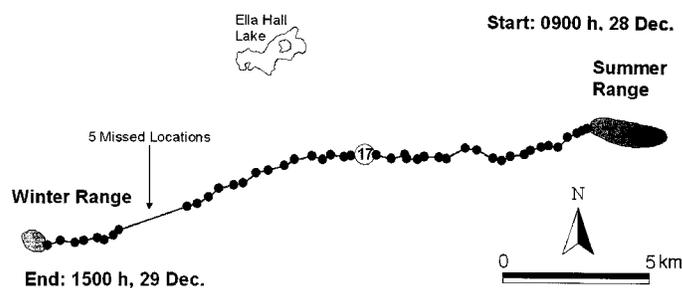


FIG. 2.—Autumn migration of female white-tailed deer 7956 from summer range to winter range in 1999 in the Superior National Forest of northeastern Minnesota based on data from a global positioning system collar. Points represent locations taken at 15-min intervals. The circle represents a pause, and the number represents h paused. The 5 missing locations resulted in a 1.5-h interval between locations. All other deer in the study were located hourly.

( $SD = 0.5$ ) during 41 of the 15-min intervals, the same as that estimated from 10 1-h intervals from the same deer (Fig. 2).

Pauses lasted a median time of 17 h (range 3–551,  $n = 7$ ). Five of the 7 pauses lasted  $<24$  h but accounted for only 7% of hours paused. Forty h (81%) of pauses lasting  $<24$  h occurred between sunset and sunrise. Median area occupied while pausing was 0.11 km<sup>2</sup> (range 0.01–1.20,  $n = 6$ ), excluding the area of a 23.0-day pause by deer 8002.

Female 7858 made a 4-km false start on 25 December when snow depth was 30 cm, but she returned to her summer range for an additional 19.0 days before migrating on 15 January. Female 8002 traveled 6 km and paused at an intermediate site for 23.0 days before resuming her migration on 21 December when snow depth was 15 cm.

## DISCUSSION

Because deer started spring migration each year at nearly the same time, with the same snow depths (0–9 cm) and affected by similar winter severity (maximum snow depths of 30 and 39 cm), we consider our analysis uninfluenced by a year effect. Autumn migration of females would appear less potentially affected by yearly differences because females are in top physical condition and severe climatic conditions generally occur well after most deer have migrated (Nelson 1995). We cannot similarly discount the effect of age. If our 1 female fawn was similar to previous fawns we have studied and accompanied her mother (Nelson and Mech 1981), then her data reflect her mother's movements. Of our other females, a 13-year-old had the fastest 1-h rate of travel (2.7 km/h), suggesting that age did not slow her down. However, it remains unknown if aging generally affects rate of travel.

Previous radiotracking research that determined locations of deer daily or weekly had to estimate the dates deer migrated to seasonal ranges (Nelson 1995; Sabine et al. 2002; Van Deelen et al. 1998). In contrast, the hourly locations of our deer more precisely measured when deer started or ended their migrations because a deer's rate of travel and its trajectory indicate when it

has switched from daily foraging and bedding on its seasonal range to linear travel away from it.

Even with hourly locations, deciding when a deer leaves or arrives on a seasonal range can be ambiguous. Deer 7920 moved 1 km away from her previous winter locations, paused for 22 h, and traveled another 1 km before pausing 21 h. She then traveled 9 km in the next 5 h before her only pause (19 h) in a 24-km migration. Her linear travel at 1.8 km/h clearly defined the start of her travel behavior, not the short moves and pauses adjacent to her winter locations. Deer 7922, 7928, and 7948 paused immediately after traveling 2–4 km away from their winter ranges. Deer 7922 paused 7 times in the next 3 km and reversed her travel to her 1st pause site but not to her winter range. Deer 7928 and 7948 traveled at rates they used in other periods of travel while migrating. The initial rate of travel by 7922 was unknown, but her 4 km of linear travel suggested she had switched from a foraging–bedding mode of behavior to a travel mode despite pausing several times within a short distance. Thus, we considered their 1st travel as the start of migration. Deer 7858 migrated to her winter range but reversed herself, moving 2 km to an area that she occupied for the next 5.0 days before returning to her winter range. We considered her arrival to be when she first reached the winter range.

We recorded a surprisingly narrow range of times of day for starting migration. One possible explanation for this may lie in the daily pattern of activity prior to migration. Deer forage most actively before and after dawn, less at midday, and actively again toward sunset (Beier and McCullough 1990; Kammermeyer and Marchinton 1977; Michael 1970). Our range of starting times and subsequent periods migrating follow a major daily feeding and rumination period (Robbins 1993) and begin at the start of an active period. Thus, deer starting migration may initially substitute migratory behavior for late afternoon foraging behavior and rumination.

*Travel rates, distances, and directionality.*—With the exception of deer 7928, our deer traveled at similar speeds over comparable distances. The data further suggest that season (spring or autumn) had no effect on rate of travel. Because we never directly observed collared deer migrating, it is conceivable that in any 1-h interval measured by GPS telemetry, deer may have combined a rapid rate of travel with a slower feeding and walking rate that resulted in the rates we measured. That our 1-h measurements represent actual rates of travel is suggested by data from deer 7956, which was located every 15 minutes. She averaged 1.6 km/h and reached 2.8 km/h in only 1 of 41 intervals. Furthermore, her locations were spaced evenly within each hour, indicating progressive movement (Fig. 2).

Further study is needed to determine what proportion of deer migrate at the slower rate of travel of deer 7928. It remains unknown why she moved more slowly than her cohorts. Her movement was as directional as theirs; on reaching her destination, she exhibited no random searching movements one might expect from a deer moving hesitantly through unfamiliar terrain.

The 1-h rates of travel seen in our study compare favorably with Rongstad and Tester's (1969) results from 9 white-tailed deer migrating at 0.8–1.6 km/h, although these authors

presented detailed travel data for only 1 female. Our further analysis of that female's data indicated that she averaged  $1.6 \pm 0.6$  km/h during 15 locations, each spaced 10–33 min apart (excluding 2 pauses and 20 min of trotting). Hourly rates of travel of deer in our study averaged roughly half the 3.6–4.0-km/h walking rates reported for caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*) measured over several hours or days (Duquette 1984; Pennycuik 1979). White and Yousef (1978) defined walking velocities of reindeer as  $<4.5$  km/h, and Fancy and White (1987) observed labored breathing and overheating above that speed.

Deer in spring migrated a median of 7.1 km/day, traveling distances 1–2 orders of magnitude shorter than the hundreds to thousands of kilometers traveled by caribou (Kelsall 1968). Female caribou migrated 7–24 km/day traveling to their calving grounds in spring (Duquette 1984; Fancy et al. 1989). Five deer in spring (63%) and 3 during autumn (75%) migrated at daily rates similar to caribou.

Although previous work documented rapid migration (Nelson 1995; Nelson and Mech 1981; Tierson et al. 1985), details of fine-scale travel along the migration track remained unknown. Our deer traveled rather linearly as they migrated, deviating only 1.2–4.0 km from the direct track toward their home ranges. This suggests that selection has favored strong spatial awareness, navigational ability, and affinity for home range location. Conceivably, the time required to wander beyond the direct approach to a home range increases predation risk in unfamiliar terrain and expends additional energy, already in limited supply for spring migrants and needed for winter survival by autumn migrants.

*Pausing and duration of migration.*—Using standard radio-tracking techniques, Nelson and Mech (1981) found that migrating deer lingered at intermediate ranges while migrating. It is clear from our current findings that such behavior is a part of a continuum where individual deer may pause frequently for periods ranging from 1 h to several days in length. Although we never directly observed deer while they paused, we presume that they were foraging and resting before traveling again. The large variation we observed in distances traveled per period, hours traveled, and time paused suggests there is no simple explanation for the timing of pauses.

Perhaps individual variation in nutritional condition leads to a varying propensity to forage and may explain why some deer pause more than others. Those deer with a greater energy deficit (Worden and Pekins 1995) may be more inclined to delay and forage more. However, deer in autumn, presumably in peak condition with maximum fat stores, paused after migrating distances and times similar to their cohorts of spring migrants (which were nutritionally stressed at the end of winter). This suggests that pausing may simply be a response to immediate hunger and fatigue, largely independent of spring or autumn energy reserves.

It also seems unlikely that pausing would somehow be related to deer encountering and being chased by wolves. Most wolf chases of deer are unsuccessful and last only a few moments, with wolves and deer resuming other behaviors when the encounter is over (Nelson and Mech 1993). Thus,

there is no evidence to suggest that the effects of a chase last for the time intervals used by pausing deer.

We found much disparity in duration of migrations, manifested by differences in number of times and hours each deer traveled and paused while migrating. Four spring migrants (7840, 7882, 7920, 7924) traveling 23–25 km at similar hourly rates of travel had a 7.5-fold maximum difference in duration of migration. Two others (7888, 7948) traveling 31–33 km at similar hourly rates had a 1.9-fold difference. The autumn migrants had a 1.8-fold difference while traveling 20–24 km, excluding deer 8002, which paused 23.0 days. For deer migrating similar distances with similar rates of travel, duration of migration is clearly determined by propensity to travel and pause. Nelson and Mech (1981) found evidence suggesting that cold temperatures increased pausing at intermediate sites and that deer migrating farther paused more. More expansive deployment of GPS collars is needed to examine these ideas as well as to determine the extent that slower travel influences duration of migration.

*Walking speed.*—Our results strongly suggest that deer travel more slowly than caribou and wildebeest while migrating. Barren-ground caribou, the most cursorial, are adapted to escape wolf predation in open country (Geist 1998). White-tailed deer are cursorial–saltatorial forest dwellers, running, jumping, and hiding to evade a wide variety of predators (Geist 1998). To the extent that selection has shaped leg and hoof morphology, walking speed is probably a partial consequence of adaptations for evading predators. Adaptation notwithstanding, given differences in habitat, the physical impedance of forest vegetation to walking by deer must also account for some difference in walking speeds between caribou and white-tailed deer.

Why has selection not favored a greater walking speed for deer since energy costs decrease with increased speed (Robbins 1993)? Possibly, the advantages of increased walking speed are balanced against decreased survival due to reduced ability to detect predators. Vigilance may influence walking speed of deer if speed at some point interferes with detecting predators. A deer walking at 4 km/h would be moving rapidly, and caribou, which have longer legs, trot and pant at speeds  $\geq 4.5$  km/h (Fancy and White 1987; White and Yousef 1978). In forest environments where visibility typically is  $< 50$  m, ability to see and hear potential predators would seem degraded as walking speeds increase. Indeed, deer fleeing from wolves look back (Mech 1970; Nelson and Mech 1993) when several hundred meters ahead of their pursuers. This suggests that knowledge of the pursuer's location takes precedence over continual rapid escape. Caribou and wildebeest inhabiting open environments can detect predators at longer distances, so their vigilance would not be impaired by increased walking speed.

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#### 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.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BEIER, P., AND D. R. MCCULLOUGH. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:1–51.
- BOWMAN, J. L., C. O. KOCHANNY, S. D. DEMARAI, AND B. D. LEOPOLD. 2000. Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin* 28:141–145.
- CARLSEN, J. C., AND R. E. FARMES. 1957. Movements of white-tailed deer tagged in Minnesota. *Journal of Wildlife Management* 21:397–401.
- COCHRAN, W. W., D. W. WARNER, J. R. TESTER, AND V. B. KUECHLE. 1965. Automatic radio-tracking system for monitoring animal movements. *BioScience* 15:98–100.
- DROLET, C. A. 1976. Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. *Canadian Field-Naturalist* 90:123–136.
- DUQUETTE, L. S. 1984. Activity patterns and their implications to the energy budgets of migrating caribou. M.S. thesis, University of Alaska, Fairbanks.
- FANCY, S. G., L. F. PANK, K. R. WHITTEN, AND W. L. REGELIN. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. *Canadian Journal of Zoology* 67:644–650.
- FANCY, S. G., AND R. G. WHITE. 1987. Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology* 65:122–128.
- GEIST, V. 1998. *Deer of the world: their evolution, behavior, and ecology*. Stackpole Books, Mechanicsburg, Pennsylvania.
- HEINSELMAN, M. L. 1996. *The Boundary Waters Wilderness ecosystem*. University of Minnesota Press, Minneapolis.
- KAMMERMEYER, K. E., AND R. L. MARCHINTON. 1977. Seasonal changes in circadian activity of white-tailed deer. *Journal of Wildlife Management* 41:315–317.
- KELSALL, J. P. 1968. *The migratory barren-ground caribou of Canada*. Canadian Wildlife Service Monograph No. 3.
- MECH, L. D. 1970. *The wolf: the ecology and behavior of an endangered species*. Doubleday, New York.
- 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.
- MICHAEL, E. D. 1970. Activity patterns of white-tailed deer in South Texas. *Texas Journal of Science* 21:417–438.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223–249.

- NELSON, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Canadian Journal of Zoology* 73:1069–1076.
- 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. 1993. Prey escaping wolves despite close proximity. *Canadian Field-Naturalist* 107:245–246.
- OLSON, H. F. 1938. Deer tagging and population studies in Minnesota. *Transactions of the North American Wildlife Conference* 3:280–286.
- PENNYCUICK, C. J. 1979. Energy costs of locomotion and the concepts of “foraging radius.” Pp. 164–184 in *Serengeti: dynamics of an ecosystem*. (A. R. E. Sinclair and M. Norton-Griffiths, eds.). University of Chicago Press, Chicago, Illinois.
- ROBBINS, C. T. 1993. *Wildlife feeding and nutrition*. 2nd ed. Academic Press, New York.
- RONGSTAD, O. J., AND J. R. TESTER. 1969. Movements and habitat use of white-tailed deer in Minnesota. *Journal of Wildlife Management* 33:366–379.
- SABINE, D. L., S. F. MORRISON, H. A. WHITLAW, W. B. BALLARD, G. J. FORBES, AND J. BOWMAN. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *Journal of Wildlife Management* 66:718–728.
- TIERSON, W. C., G. F. MATTFELD, R. W. SAGE, AND D. F. BEHREND. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *Journal of Wildlife Management* 49:760–769.
- VAN DEELEN, T. R., H. CHAMPA III, M. HAMADY, AND J. B. HAUFLE. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *Journal of Wildlife Management* 62:205–213.
- VERME, L. J. 1973. Movements of white-tailed deer in upper Michigan. *Journal of Wildlife Management* 37:545–552.
- WHITE, R. G., AND M. K. YOUSEF. 1978. Energy expenditure in reindeer walking on roads and tundra. *Canadian Journal of Zoology* 56:215–223.
- WORDEN, K. A., AND P. J. PEKINS. 1995. Seasonal change in feed intake, body composition, and metabolic rate of white-tailed deer. *Canadian Journal of Zoology* 73:452–457.

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