MOVEMENT OF FEMALE WHITE-TAILED DEER: EFFECTS OF CLIMATE AND INTENSIVE ROW-CROP AGRICULTURE

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Abstract: Movements (e.g., migration, dispersal) of white-tailed deer (*Odocoileus virginianus*) vary greatly over the geographic range of the species. Therefore, region-specific, empirical information is needed to effectively manage deer populations. Movements of white-tailed deer have been well documented in forest dominated habitats; however, little information related to white-tailed deer movements exists in intensively (>80%) cultivated areas. From January 2001 to August 2002, we monitored movements of 77 (61 adult, 16 young) female white-tailed deer in southwest Minnesota. We collected 6,867 locations, calculated 130 home ranges, and documented 149 seasonal movements. Fifteen percent of deer were nonmigratory, whereas 35% were facultative migrators, and 42.5% were obligate migrators. Mean distance between summer and winter home range was 10.1 km. Temperature and snow depth had the greatest influence on initiation of seasonal migration, whereas crop emergence and harvest had minimal effects. Four deer (8%) dispersed a mean distance of 71.3 km with 1 adult female moving a straight-line distance of 205 km. All dispersing deer occupied a temporary staging area for approximately 1 month between previous winter and new summer ranges. Mean home range (95% use area) in winter (5.2 km^2) was over twice as large as home range in summer (2.3 km^2). Movements exhibited by white-tailed deer in southwest Minnesota were influenced by large annual fluctuations in climate and a highly fragmented landscape dominated by row-crop agriculture. We provide data beneficial to biologists managing northern populations of white-tailed deer in fragmented environments by detailing the relationship between climate, intensive agriculture, and deer movements.

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Key words: agriculture, dispersal, home range, migration, Minnesota, movement, *Odocoileus virginianus*, white-tailed deer.

Seasonal migration is common among cervids (Wallmo and Regelin 1981, Fancy et al. 1989, Demarais et al. 2000, Hjeljord 2001, Irwin 2002). Northern cervid populations migrate annually in response to changes in availability and quality of food supplies and severe winter weather (Marchinton and Hirth 1984, Sandegren et al. 1985, Irwin 2002). Similarly, research on white-tailed deer indicated onset of cold temperatures and depth of snow exert the greatest influences on seasonal movement from summer to winter home ranges (Verme 1968, Ozoga and Gysel 1972, Verme 1973, Blouch 1984, Nelson 1995). For instance, Tierson et al. (1985) and Nelson (1995) reported that temperatures below –7°C initiated autumn migration. Also, the effective critical temperature for adult female deer was calculated at –7°C (DelGiudice 2000). At or below this temperature threshold, heat losses may exceed energy expenditures for standard metabolism and activity, and an increase in metabolism is needed to maintain homeothermy (McDonald et al. 1973).

In addition to decreased temperatures, increased snow depths were reported to initiate migration to winter range. In New Brunswick, Drolet (1976) estimated the snow depth threshold for the initiation of migration was 30.4 cm, and Sabine et al. (2002) determined peak migration coincided with accumulation of 40 cm of snow. Nelson and Mech (1981) reported 35–40 cm of snow initiated migration in northern Minnesota. Further, Kelsall (1969) noted that deer were restricted in movement when snow depth exceeded 40 cm (i.e., about 20 cm less than mean deer chest height).

During mild winters with below average snowfall, deer may occupy summer range year-round or only briefly occupy a winter range (Drolet 1976, Blouch 1984, Nelson 1995). White-tailed deer exhibit high site fidelity and were reported to move through suitable habitat en route to traditional seasonal range (Tierson et al. 1985).

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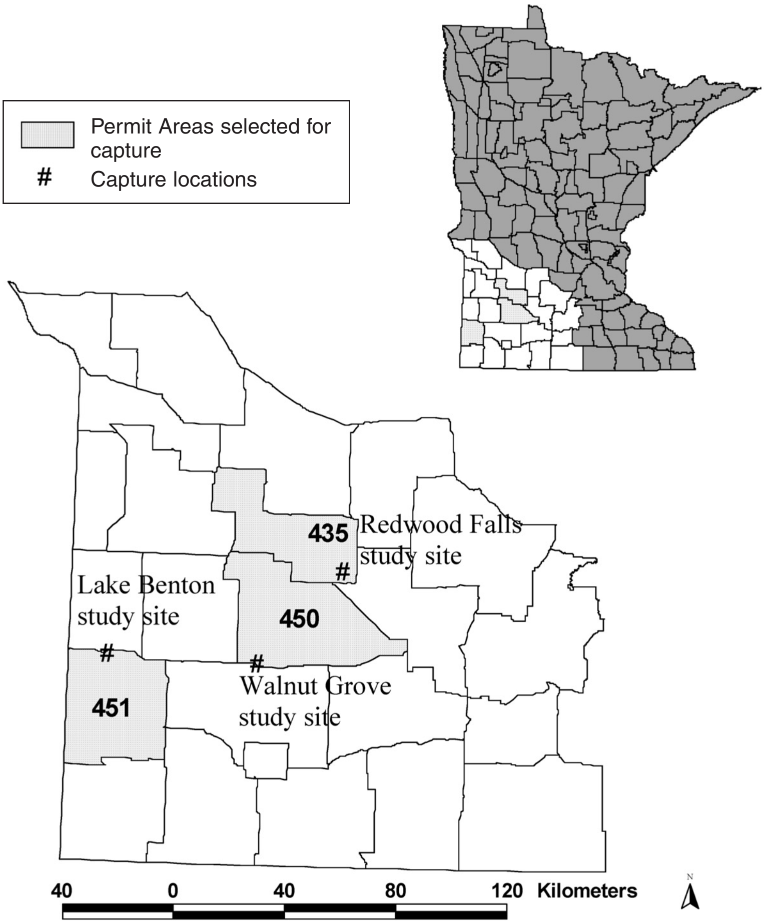

Fig. 1. Study area and white-tailed deer capture locations in southwest Minnesota, USA, 2001–2002.

predictions based on data collected for 1 population are often not reliable for others.

Movements of white-tailed deer are well documented in forested habitat throughout the northern portion of their range (Rongstad and Tester 1969, Tierson et al. 1985, Fuller 1990, Nelson 1995, Filipiak 1998, Sabine et al. 2002); however, data on movements are limited in intensively farmed areas (Nixon et al. 2001). Specifically, data are limited on migration and dispersal in agricultural areas in the northern range of white-tailed deer. Thus, our objectives were to determine seasonal movement patterns (i.e., migration, dispersal) and home ranges of white-tailed deer in southwest Minnesota. We tested for effects of climate on movement behavior of female white-tailed deer in a landscape dominated by row-crop agriculture. We hypothesized that (1) because of the effects of low temperatures and snow depth, migration behavior (e.g., rate, time of departure) of deer occupying the northern Midwest Agricultural Region would be similar to that in forested areas with similar climates, rather than agricultural areas with milder climates; and (2) because of limited permanent cover in highly fragmented landscapes dominated by row-crop agriculture, dispersal of deer occupying the northern Midwest Agricultural Region would be similar to that in other intensively farmed areas, rather than forest dominated habitat in the north.

Young (<1-yr-old) and yearlings (between 1- and 2-yrs-old) may disperse, moving from natal home ranges and establishing permanent ranges elsewhere (Nixon et al. 1991, Nelson 1993). Amount of dispersal occurring between deer populations determines emigration and immigration rates and may represent a significant exchange of individuals across management boundaries (Rosenberry et al. 1999).

Because of difficulty in monitoring animals that travel long distances, empirical data documenting movement that occurs across landscapes is not available in many areas, particularly in intensively farmed regions (Nixon et al. 1991). Managers typically ignore dispersal, or they assume that immigration and emigration are equal (Johnson 1994, Rosenberry et al. 1999). In addition, movements of white-tailed deer can vary over their geographic range (Marchinton and Hirth 1984, Demarais et al. 2000) and among individuals (Sabine et al. 2002); therefore,

STUDY AREA

We conducted the study in 34,627 km^2 of southwest Minnesota (43° 29′N to 45° 16′N – 93° 38′W to 96° 27′W) containing 24 deer Permit Areas (PAs; Fig. 1). In Minnesota, deer population models and local manager recommendations were used to determine the number of antlerless deer harvest permits allocated in each PA. Topography of the region was flat to rolling, with elevations from 229 to 608 m above mean sea level. Climate in southwest Minnesota was subhumid continental, with warm summers and cold winters. Mean daily temperature during July and January was 23.1°C and –9.8°C, respectively, and average annual precipitation and snowfall was 65.4 cm and 105.2 cm, respectively (Midwest Regional Climate Center 2002). Land cover was dominated by row-crop agriculture (86%), primarily corn and soybeans (Minnesota Department of Natural Resources 2000). Spring planting was generally completed in May, and crops emerged during early June (Minnesota Agricultural Statistics Service 2003). Corn and soybean harvest began in October and was generally completed by early November. In autumn, tillage was the prevalent practice; soybean fields were disked, and cornfields were disked and plowed. Only a small percentage of cropland was unharvested or left as stubble.

Other land cover (excluding land types covering <0.5% of study area [e.g., bare rock/industrial]) included grassland (6.5%), forest (3%), open water (1.6%), and wetlands (0.8%; Minnesota Department of Natural Resources 2000). In areas difficult to farm (e.g., steep slopes, poorly drained sites), grasslands consisted of cool and warm season grasses including smooth brome (*Bromus inermis*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), tall dropseed (*Sporobolus asper*), and sideoats grama (*Bouteloua curtipendula*; Johnson and Larson 1999).

In riparian-forested areas, dominant overstory vegetation included eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), basswood (*Tilia americana*), and bur oak (*Quercus macrocarpa*; Minnesota Association of Soil and Water Conservation Districts Forestry Committee 1986). Shelterbelts adjacent to farmsteads were composed of spruce (*Picea* spp.), cedar (*Juniperus* spp.), Douglas fir (*Pseudotsuga menziesii*), and silver maple (*Acer saccharinum*; Minnesota Association of Soil and Water Conservation Districts Forestry Committee 1986), with an understory dominated by smooth brome and other grasses (e.g., bluegrass [*Poa* spp.], fescue [*Festuca* spp.], switchgrass).

METHODS

We captured female white-tailed deer by net-gun deployed from a helicopter (Krausman et al. 1985) in deer wintering areas (Marchinton and Hirth 1984) at 3 study sites (Lake Benton, Redwood Falls, Walnut Grove; Fig. 1) in southwest Minnesota during 22–24 January 2001 and 26 January 2002. We restrained, blindfolded, and transported each captured deer to a nearby processing site (<2 km). We aged deer as young (~8-months-old) or adult (>1-year-old) by noting body size and lower incisor wear. We ear-tagged, measured, physically examined, and radiocollared each deer. We continuously monitored rectal temperature as an indicator of physical stress. If rectal temperature exceeded 40°C, we used snow or ice to cool animals. If the rectal temperature did not decrease, we released the deer. We attached radiocollars (Advanced Telemetry Systems, Isanti, Minnesota, USA) to deer. The collars were equipped with activity and mortality sensors and switched to mortality mode after the transmitter remained still for ≥8 hours. Prior to release, we administered a 5-cc intramuscular injection of a broad-spectrum antibiotic (Dual-Cillin, Phoenix Scientific, St. Joseph, Missouri, USA) to deer and removed blindfolds and restraint straps. Our methods were approved by the Institutional Animal Care and Use Committee at South Dakota State University (No. 00–A038).

We monitored radiocollared deer for mortality 2–3 times per week and located them by ground triangulation twice per week. We estimated azimuths (3–5) from established telemetry stations using a vehicle-mounted, null-peak antenna with an accuracy of ±1.0° (Brinkman et al. 2002, Cox et al. 2002). If we could not locate deer from the ground, we used fixed-wing aircraft. We assigned Universal Transverse Mercator (UTM) coordinates to locations of individuals we visually observed. We used a maximum likelihood estimator procedure to calculate deer locations by entering azimuths into the computer program Locate II (Nams 2001) and plotting locations on U.S. Geological Survey, 3-meter Digital Orthophoto Quadrangles using ArcView software (ESRI, Redlands, California, USA). We used the fixed-kernel method (Seaman et al. 1999) to calculate 95% home ranges and 50% core areas with the spatial movement analysis extension in ArcView. We defined dispersal as permanent movement of individual deer away from established annual home ranges to new, nonoverlapping annual home ranges (Marchinton and Hirth 1984). Because natal summer range of captured deer was unknown, we assumed (1) deer that established new winter ranges were dispersers and had established new summer ranges the previous season, and (2) deer that occupied a summer range for ≥1 month and then moved away from this range with no return also were dispersers. We defined migration as seasonal movement between nonoverlapping winter and summer ranges, measured as linear distance between centers of seasonal home ranges. If we detected overlap between seasonal home ranges, we assumed migration did not occur (Nicholson et al. 1997). We considered deer obligate migrators (Sabine et al. 2002) if they migrated between established winter and summer ranges during every migratory period. We considered deer facultative migrators if they failed to migrate to a winter range, migrated briefly (<1 month) to a winter range, or made several migrations between seasonal ranges during a single winter (Nelson 1995). We considered deer residents (VerCauteren and Hygnstrom 1998) if they never migrated. We only assigned a migration strategy to individuals monitored through 3 consecutive migratory periods. We defined seasonal movement from winter to summer range as spring migration, and movement from summer to winter range as autumn migration.

To determine whether temperature and snow depth influenced migration of white-tailed deer, we derived a deer winter severity index from the literature (Kelsall 1969, Drolet 1976, Nelson and Mech 1981, Tierson et al. 1985, Nelson 1995, Sabine et al. 2002). We used this index to winter severity to analyze the relationship between movement data and climate (National Oceanic and Atmospheric Administration 2002). To calculate our index of winter severity, we accumulated 1 point for each day mean ambient temperature was ≤–7°C, and we accumulated an additional point for each day snow depth was ≥35 cm.

We compared deer migration distances, home ranges, and winter severity indices between seasons and years using *t*-tests. We compared differences in migration distances, percent of deer migrating, home ranges, and deer winter severity indices between study sites using the Kruskal-Wallis rank sum chi-square test with SYSTAT 9.0 (Wilkinson 1990). We used a variation of Sheppard's correction, which allows measurement of deer departure dates from seasonal ranges during unequal intervals (Johnson et al. 2004). We set α at $P \leq 0.05$, and a Bonferroni correction factor was used to maintain the experiment-wide error rate when multiple chi-square and *t*-tests were performed (Neu et al. 1974).

RESULTS

We captured and radiocollared 77 deer (61 adult, 16 young) during January 2001 ($n = 58$) and 2002 ($n = 19$). We captured 31 deer at Lake Benton, 19 at Walnut Grove, and 27 at Redwood Falls (Fig. 1). We collected 6,867 deer locations with a mean 95% error ellipse of 3.8 ha. We documented 149 seasonal movements during 3 migratory periods: spring 2001, autumn 2001, and spring 2002. We monitored 40, 3, and 25 individual deer through 3, 2, and 1 migratory period(s), respectively. We calculated 130 individual home ranges during 4 seasonal periods: winter 2000–2001, summer 2001, winter 2001–2002, and summer 2002. We calculated 1, 27, 11, and 23 home range(s) for individual deer during 4, 3, 2, and 1 seasonal range period(s), respectively.

Seasonal Migration and Dispersal

Spring 2001.—Forty deer (76%) migrated a mean distance of 8.8 km (SE = 1.1 km, range = 1.6–30.8 km). Mean distance migrated ($\chi^2_2 = 0.997$, $P = 0.608$) and percentage of deer migrating ($\chi^2_2 = 2.869$, $P = 0.238$) were similar among sites. Nine deer (17%) did not migrate and used part of their winter range as summer range. Four deer (8%; 2 young, 2 adults) dispersed and established permanent ranges elsewhere. Before dispersing, each deer migrated to a staging area we assumed was a previous summer range and remained there for ~1 month. This behavior was not identified among migrating deer. Mean dispersal distance was 71.3 km (SE = 45.1 km) and ranged from 16 to 205 km. Two dispersals occurred at Redwood Falls, 1 at Walnut Grove, and 1 at Lake Benton. Median departure date for migrating and dispersing deer was 8 April ($n = 44$, SD = 18.3) and ranged from 10 March to 25 May.

Autumn 2001.—We monitored 43 deer during autumn 2001. Twenty-three (54%) deer migrated a mean distance of 11.2 km (SE = 1.7, range = 1.6–30.4). The remaining 20 deer were nonmigratory. Mean migration distance ($\chi^2_2 = 0.205$, $P = 0.903$) and percentage of deer migrating ($\chi^2_2 = 0.760$, $P = 0.684$) were similar among sites. Median departure date for migratory deer was 28 November ($n = 21$, SD = 10.9) and ranged from 31 October to 22 December. We were unable to determine departure date of 2 deer. Of the 40 deer that migrated during spring 2001, we monitored 31 during autumn 2001, whereas the fate of the remaining 9 deer was death ($n = 8$) or radiocollar malfunction ($n = 1$). Of 31 deer monitored that were previous migrators, 21 (68%) migrated a mean distance of 10.6 km (SE = 1.5) back to their previous winter range, and 10 (32%) remained on summer range throughout winter 2001–2002. Of the 4 dispersals monitored during spring 2001, 2 deer migrated a mean distance of 17.9 km (SE =

12.5) to a new home range during autumn 2001 and 2 remained on their current summer range. All nonmigratory individuals monitored during spring 2001 (n = 9) that we monitored during autumn 2001 (n = 8) remained nonmigratory.

Spring 2002.—Because we captured and radiocollared additional deer during winter 2001–2002, we monitored 55 deer during spring 2002. Thirty-two (58%) deer migrated a mean distance of 10.8 km (SE = 1.2, range = 2.0–29.9). Mean distance migrated was similar (χ^2_2 = 0.351, P = 0.839) among sites. In addition, migration distance was similar (t = –1.28, df = 70, P = 0.205) during spring 2001 and 2002. Because we did not monitor deer during autumn migration 2002, we were unable to determine spring 2002 dispersal. Unlike deer that dispersed during 2001, none of the migrating deer captured during winter 2001–2002 occupied 2 separate ranges during summer 2002; thus, they were all likely migrators rather than dispersers. Twenty-three (42%) deer did not migrate during spring 2002. The percentage of deer migrating varied by site, with more deer migrating at Lake Benton (83%; χ^2_2 = 9.527, P = 0.009) than Walnut Grove (42%), or Redwood Falls (40%). Median date of departure from winter range was 18 April (n = 27, SD = 16.2) and ranged from 31 March–30 May. Of 23 (42%) deer that did not migrate, 4 were migratory and 15 were nonmigratory during autumn 2001. We captured the remaining 4 deer during winter 2001–2002. Six of 7 deer that did not migrate during spring 2001 remained nonmigratory.

Of 40 deer that we continuously monitored through 3 migratory periods (i.e., spring 2001, autumn 2001, spring 2002), 17 (42.5%) were obligate migrators, 14 (35%) were facultative migrators, 6 (15%) were permanent residents, and 3 (7.5%) dispersed during the spring 2001 migratory period and were not classified as having a migration strategy. Mean distance migrated was 11.8 km (SE = 1.7) and 4.2 km (SE = 0.4) for obligate and facultative migrators, respectively. During spring 2001, median departure date for obligate and facultative migrators was 9 April (n = 15) and 4 April (n = 16), respectively. During spring 2002, median departure date of obligate and facultative migrators was 24 April (n = 10) and 12 April (n = 6), respectively. Median spring departure date for obligate migrators was 5 and 12 days earlier than that for facultative migrators during 2001 and 2002, respectively.

Home Range

We calculated seasonal home ranges of individual deer using a minimum of 25 and a mean of 37.3 (n = 130 home ranges, SE = 0.8) locations. We were unable to test for differences in sizes of home ranges during winter between years because of an insufficient sample size (n = 2) during winter 2000–2001. Mean home-range size during summer was similar between years (t = 1.553, df = 91, P = 0.124). Mean home-range size, however, was larger (t = –3.65, df = 128, P < 0.001) during winter than summer; thus, seasons were analyzed separately.

Mean home range and core area of deer in winter were 5.2 km^2 (n = 37, SE = 0.8, range = 0.4–18.7) and 0.8 km^2 (n = 37, SE = 0.1, range = 0.1–3.4), respectively, and home ranges were similar (χ^2_2 = 1.995, P = 0.369) among study sites. Mean summer home ranges and core areas were 2.3 km^2 (n = 93, SE = 0.2, range = 0.4–12.8) and 0.3 km^2 (n = 93, SE < 0.1, range = <0.1–2.0), respectively, and home ranges were similar (χ^2_2 = 5.246, P = 0.073) among sites. Mean annual home range and core area were 3.1 km^2 (n = 130, SE = 0.3, range = 0.4–18.7) and 0.5 km^2 (n = 130, SE < 0.1, range = <0.1–3.4), respectively.

Winter Severity Index Effects

We calculated a deer winter severity index for each study site during November–March. During October and April, no days were reported with temperatures below –7°C, and snow depth never exceeded 35 cm (National Oceanic and Atmospheric Administration 2002). Because these months had a deer winter severity index of zero, we did not include them in winter severity analyses. Deer winter severity index was highest at Lake Benton during winter 2000–2001 (χ^2_2 = 40.020, P < 0.001) but was similar across study sites during winter 2001–2002 (χ^2_2 = 4.612, P = 0.100; Fig. 2). Across all study sites, the cumulative deer winter severity index score was 2.7 times greater (t = 14.07, df = 1810, P < 0.001) in 2000–2001 (139) than 2001–2002 (51; Fig. 2).

Autumn migration coincided with accumulation of snow and decreasing temperatures. Following a winter storm during 26–28 November 2001, 10 of 21 deer (52%) with known departure dates initiated migration (Fig. 3). Migration was in response to snow depths of 36 cm at Lake Benton and Walnut Grove and 16 cm at Redwood Falls. Mean ambient daily temperatures during this migration event were –4°C to –6°C and were the lowest temperatures recorded up to that date.

Spring migration also coincided with changes in temperature and snow depth (Figs. 4, 5). Movement was less abrupt, however, compared with autumn migration. During winter 2000–2001, Lake Benton and Walnut Grove had higher (χ^2_2 = 100.040, $P <$ 0.001) deer winter severity indices than Redwood Falls. Thus, we analyzed factors influencing spring migration separately. Nine (29%) deer at Lake Benton and Walnut Grove departed winter range during late March 2001 within 1–4 days of mean daily temperatures increasing and remaining above –9°C, and snow depths declining below 30 cm (Fig. 4). An additional 8 (26%) deer migrated during the first week of April, following a week of temperatures ≥0°C and a decrease in snow depth from 28 to 0 cm.

Factors influencing spring migration in 2001 at Redwood Falls were less apparent (Fig. 4). Departure from winter range occurred between 10 March and 18 May with 2 individuals migrating in response to temperatures and snow depths that initiated migration in other sites. Compared with Walnut Grove and Lake Benton, Redwood Falls experienced milder and more gradual changes in weather conditions with few days where temperatures and snow depths reached thresholds necessary to promote migration.

Winter 2001–2002 was milder across all study sites compared with 2000–2001. In 2002, 37% (n = 10 of 27) of deer migrated during the first week of April following a 10–15°C rise in mean ambient temperature across all study sites; temperatures increased from –6°C on 3 April to 4–9°C on 7 April (Fig. 5). Snow depths were minimal (5 cm) and likely played less of a role in initiating migration. The second group to migrate simultaneously departed between 1 and 3 May (Fig. 5). No sudden shift in temperature coincided with this migration, nor was there any snow accumulation at this time. A minor snowfall (2–5 cm) occurred on 28 April but melted the following day.

DISCUSSION

Seasonal Migration

Mean (10.1 km) distance migrated by white-tailed deer in southwest Minnesota was slightly lower than reported for other northern populations subject to cold winter temperatures (23.2 km, Sparrowe and Springer 1970; 13.8 km, Verme 1973; 20.7 km, Hoskinson and Mech 1976; 11.0 km, Simon 1986; 15.7 km, Sabine et al. 2002) and populations in other intensively farmed areas with milder climates (13.0 km, Nixon et al. 1991). Compared with previous reports, our data indicate that land cover differences (e.g., row crop agriculture vs. forest) do not directly influence migration distance. A higher percentage of deer migrated in our study (54–75%) compared to that reported (20%) by Nixon et al. (1991) for an intensively farmed region of Illinois. This was probably because our study area experienced colder winters with more snow accumulation. As found in northern white-tailed deer studies conducted in forested areas (Verme 1968, Ozoga and Gysel 1972, Blouch 1984, Beier and McCullough 1990, Nelson 1995), we concluded that fluctuations in temperature and snow depth exerted the

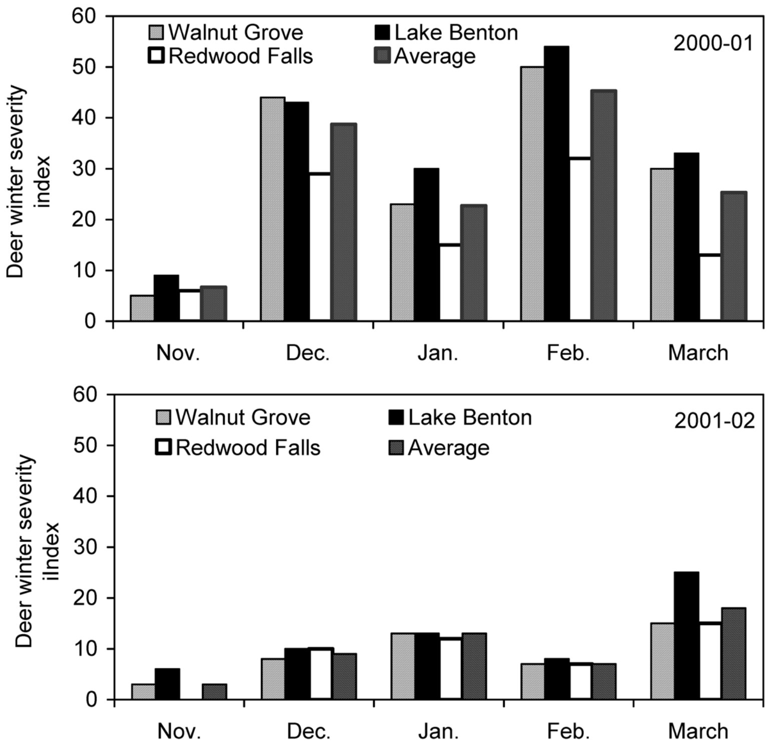

Fig. 2. Monthly deer winter severity index for individual study sites in southwest Minnesota, USA, 2000–2002. (One point accumulated for each day with an ambient temperature ≤–7°C and an additional point accumulated for each day with snow depths ≥35.0 cm; National Oceanic Atmospheric Administration 2002).

strongest effects on seasonal movement in the far northern reaches of areas with intensive row-crop agriculture. Thus, the effects of climate on seasonal migration were likely more significant than the effects of agricultural practices, despite the dominant row-crop (80%) land cover. In addition, because seasonal migrations were completed before crop emergence and after crop harvest, crop phenology likely had minimal effects on timing of migration.

During 2001, average harvest completion date for 90% of the corn and soybeans was 5 November and 22 October, respectively (Minnesota Agricultural Statistics Service 2003), whereas median date of autumn migration was 28 November (n = 21). Likewise, crop planting and emergence did not seem to influence spring migration. Median date of winter range departure was 8 April in 2001 (n = 44) and 18 April in 2002 (n = 27), whereas the 2001 and 2002 average planting completion date for 90% of the corn was 27 May and 19 May, respectively, and the average date for soybeans was 10 June and 31 May, respectively (Minnesota Agricultural Statistics Service 2003).

Mixed strategies of seasonal migration have been well documented among white-tailed deer (Sparrowe and Springer

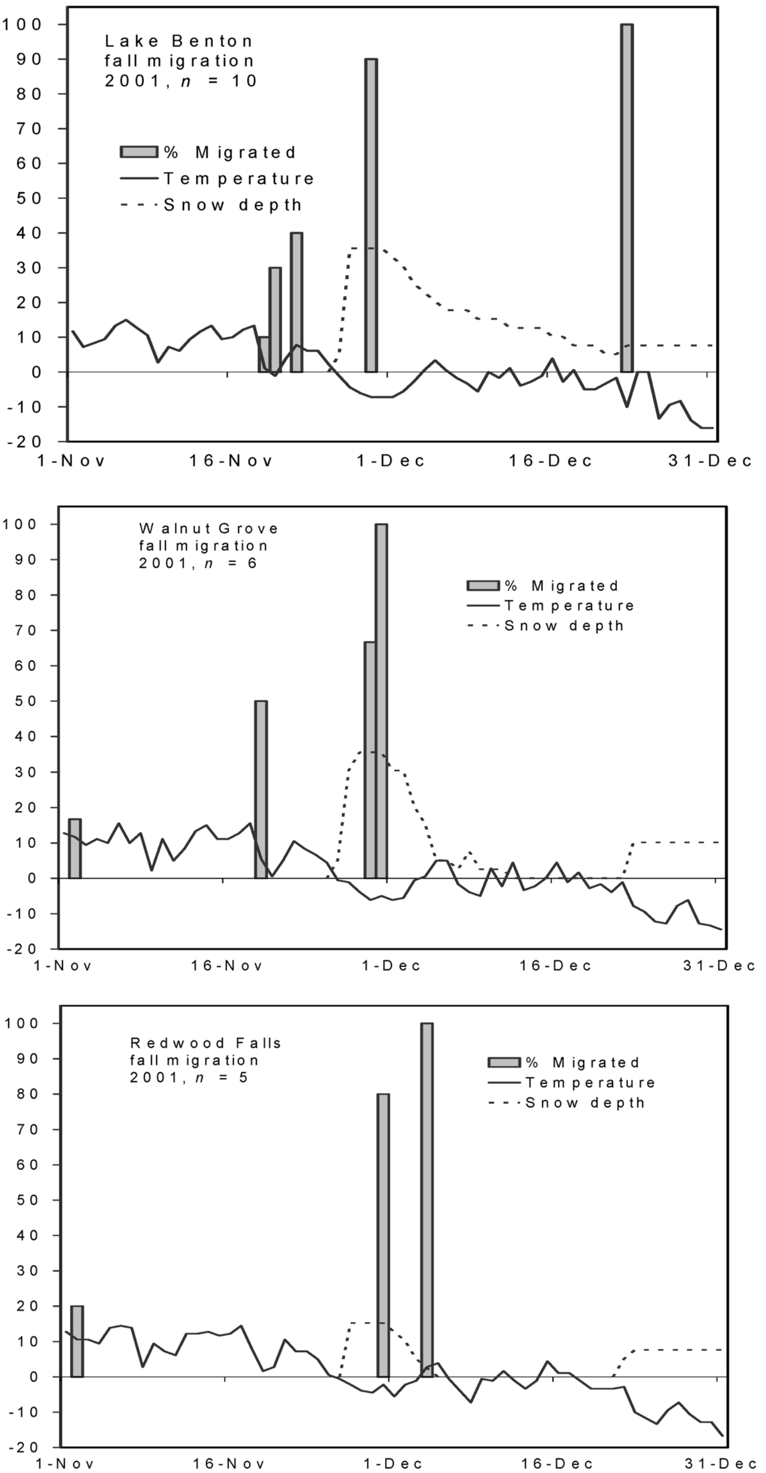

Fig. 3. Autumn migration events by study site for radiocollared female white-tailed deer in southwest Minnesota, USA, 2001. The Y-axis is shared by all 3 variables (i.e., temperature [C°], snow depth [cm], percentages of deer migrating [%]). A migration event represents the cumulative percentage of migrating individuals at each study site with known departure dates from summer range.

1970, Drolet 1976, Blouch 1984, Nelson 1995, VerCauteren and Hygnstrom 1998, Sabine et al. 2002). Our results support these earlier findings. In southwest Minnesota, migration strategies for female deer included obligate migrators, facultative migrators, and permanent residents. Nicholson et al. (1997) reported that mule deer (*O. hemionus*) maintained a strategy of mixed migration in areas with variable precipitation and snow cover. Drolet (1976), Blouch (1984), and Nelson (1995) reported that during mild winters with below average snowfall, deer may occupy the same range year round or become facultative migrators. A lower deer winter severity index in all study sites during winter 2001–2002, relative to the deer winter severity index during 2000–2001 (Fig. 2), may explain why 32% of individuals did not return to winter range during autumn 2001 and exhibited facultative migration. Some facultative migrating deer returned to winter range in 2001–2002 for a brief period; others made several trips between summer and winter range.

Explanations for the variation in the prevalence of facultative migration among deer have been speculative. Nelson (1995) suggested that differences in hunting mortality on summer

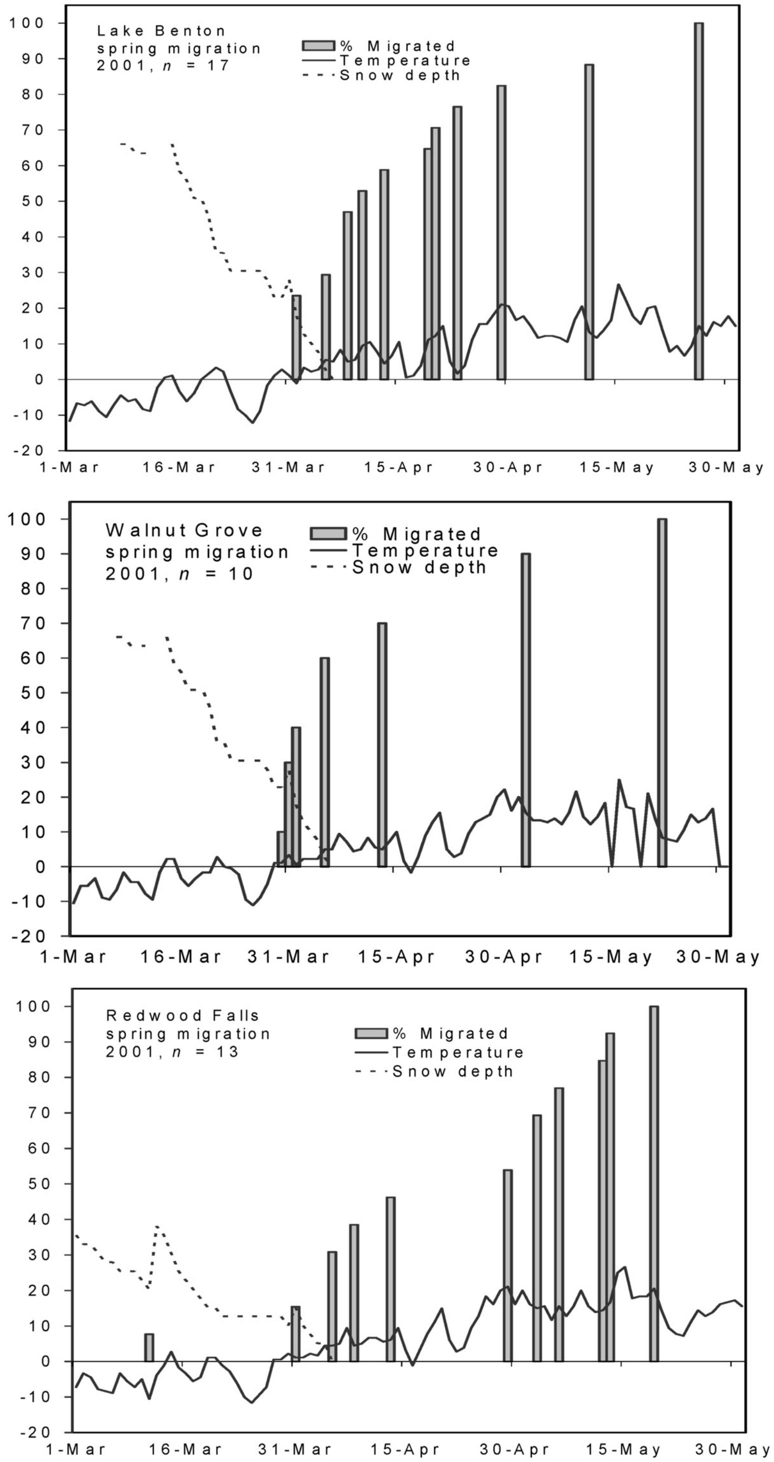

Fig. 4. Spring migration events by study site for radiocollared female white-tailed deer in southwest Minnesota, USA, 2001. The Y-axis is shared by all 3 variables (i.e., temperature [C°], snow depth [cm], percentage of deer migrating [%]). A migration event represents the cumulative percentage of migrating individuals at each study site with known departure dates from winter range.

range and lower population size and density may influence migration among deer in adjacent wintering areas. Sabine et al. (2002) suggested that differences in behavior among individual deer were influenced by migration distance. Our data supports the suggeston of Nicholson et al. (1997) that variability in climate ultimately might be responsible for a mixed-migration strategy.

Late-season migrators are likely influenced less by low ambient temperatures and snow depths. These deer remain on winter range well into spring thaw, after snow has melted and temperatures have risen and remained above 0°C. Migration among these animals was potentially initiated by plant phenology (Nixon et al. 1991), pre-parturition (Ozoga et al. 1982, Simon 1986), or seasonal stimuli (Sabine et al. 2002). If late season migrators were less sensitive to winter severity, then these deer may be more likely to be obligate rather than facultative migrators. Our results support this notion in that median departure date for obligate migrators was 5 days after facultative migrators during spring 2001 and 12 days after facultative migrators during spring 2002.

We did not monitor deer daily; therefore, the number of days between departure and arrival on seasonal ranges was un-

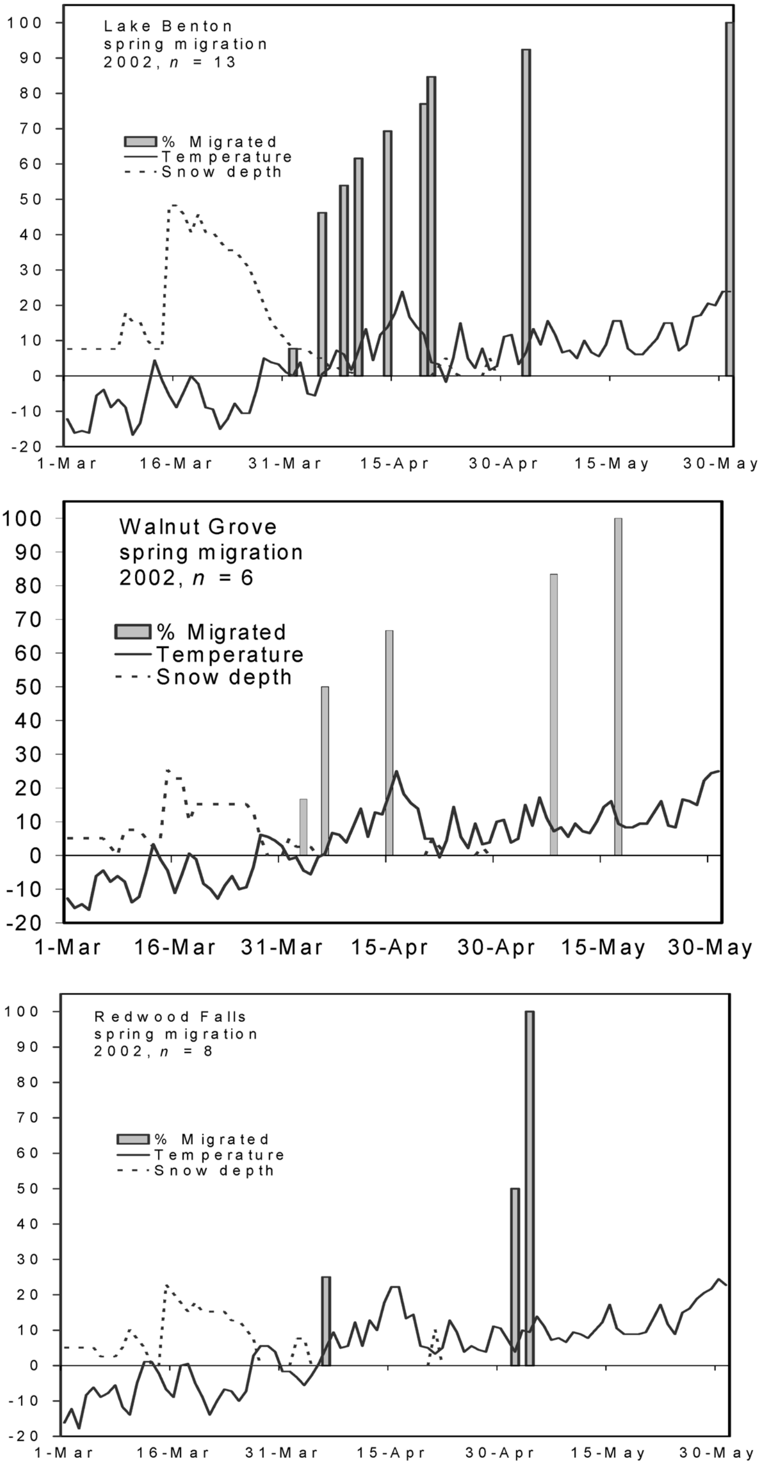

Fig. 5. Spring migration events by study site for radiocollared female white-tailed deer in southwest Minnesota, 2002. The Y-axis is shared by all 3 variables (i.e., temperature [C°], snow depth [cm], percentage of deer migrating [%]). A migration event represents the cumulative percentage of migrating individuals at each study site with known departure dates from winter range.

known. However, there was minimal meandering between seasonal ranges, and most females that we monitored completed migrations, regardless of distance, in <1 week. Nixon et al. (1991) noted rapid migration in Illinois with deer settling on summer ranges within 10–12 days of initial movement. In northeast Minnesota, migrations from winter yards were completed in <2 weeks (Nelson and Mech 1981). Similarly, in the central Black Hills of South Dakota, spring migrations of white-tailed deer from low-elevation winter ranges to high-elevation summer ranges were completed within 1 week (DePerno 1998, DePerno et al. 2002).

Dispersal

Annual dispersal of female white-tailed deer is common within the Midwest Agricultural Region (Gladfelter 1984). Fifty percent of young females and 21% of yearling females dispersed each spring in Illinois (Nixon et al. 1991). During spring 2001, 17% of young females and 5% of adult females dispersed in southwest Minnesota.

Migration and dispersal events can occur for individual deer during a single season, but timing and stimuli of these events differ. For instance, dispersing deer had strikingly different winter range departure behavior from migrating individuals. All dispersers (2 young, 2 adults) migrated to a temporary staging area before dispersing to new permanent ranges. For example, an adult deer (D591) departed from winter range on 12 April 2001 and moved 22 km. It remained on this staging area until 19 June, and then moved again. We next located D591 on 2 December 2001 in eastern South Dakota, approximately 205 km from previous winter range; this represents one of the longest dispersal distances reported for white-tailed deer. Sparrow and Springer (1970) reported a young female moving 224 km from South Dakota into Iowa over 35 months. Kernohan et al. (1994) reported a dispersal distance of 213 km for a yearling male in northeast South Dakota, and Sparrow and Springer (1970) reported an adult male dispersal of 203 km and a yearling female dispersal of 161 km in eastern South Dakota. Nelson (1993) reported a dispersal distance of 168 km in northeastern Minnesota. Another adult deer (D372) that dispersed exhibited behavior similar to D591. Deer 372 departed from winter range on 19 April and we relocated it on 9 May, 6 km from its previous location. Deer 372 remained on this temporary staging area until 20 May, moved back to previous winter range for 5 days, and then dispersed 19 km to a new permanent summer range. The other 2 dispersers were 10–11 months of age. Each young deer also established a temporary staging area approximately 1 month before dispersing 46 and 16 km, respectively, to new summer ranges.

Social pressures were identified as the primary stimuli for dispersal (Marchinton and Hirth 1984). Near parturition, females often run off young from the previous year, encouraging them to disperse (Downing and McGinnes 1969). We observed this behavior at night under spotlight while searching for white-tailed deer neonates. Pregnant females flailed their forelegs when approached by year-old deer or chased them away. This aggressive behavior may explain the use of staging areas by dispersing young ($n = 2$). In southwest Minnesota, peak migration occurred >1 month prior to parturition; therefore, a window seems to exist between the time when the pregnant female arrives on summer range and the time just before parturition when her previous young are forced to disperse. In addition, dispersal behavior among young deer is rare before 11 months of age (Nixon and Etter 2001). In general, 10- to 11-month-old deer follow their mothers to summer range and remain there for about 1 month (i.e., this servesa as a staging area) until they are chased off prior to parturition. In intensive agricultural areas with limited available cover in spring, these young deer often must travel long distances before finding suitable habitat not occupied by other females (Demarais et al. 2000, Nixon et al. 2001).

Explanations for adult female ($n = 2$) dispersal are more complicated. Although exact ages of these deer were unknown, it was possible that 1 or both were yearlings. If so, it was possible this was their initial pregnancy, and they dispersed to seek solitude to fawn. Ozoga et al. (1982) suggested that isolation is essential for proper mother-infant bond formation. In nutrient-rich landscapes (e.g., southwest Minnesota), competition among females for parturition sites may be more important than competition for food, and white-tailed deer will forcefully defend parturition grounds (Nixon et al. 1991, 2001). Matriarch females defend the same parturition area annually (Ozoga et al. 1982). Furthermore, because of difficulty establishing parturition grounds in highly fragmented agricultural environments with limited cover, dispersing adult females may be forced to move large distances before finding suitable habitat.

Unsuccessful reproduction is another reason adults may have dispersed. Ozoga et al. (1982) noted that unsuccessful mothers fail to exhibit any prolonged isolation or aggressive behavior. Without neonates, adult females lack the innate behavior to defend parturition sites, and barren females often revert to the social position of a young deer (Ozoga and Verme 1986, Nixon et al. 1991). Therefore, adult females may have dispersed to avoid confrontation with females rearing young.

Home Range

In northern regions, snow depth, deer density, and low temperatures have the greatest influence on daily activity of white-tailed deer (Verme 1973, Tierson et al. 1985, Beier and McCullough 1990). In response to severe weather conditions, deer minimize movement to conserve energy (Moen 1976, Parker et al. 1984). Hence, it is predicted that white-tailed deer have smaller ranges in winter than in summer. In forested regions of New York (Tierson et al. 1985) and Minnesota (Nelson and Mech 1981, Mooty et al. 1987), mean winter ranges were approximately half the size of summer ranges. In southwest Minnesota, however, mean winter home range (5.2 km^2, $n = 37$) was more than double mean summer home range (2.3 km^2, $n = 93$). Our results were similar to those in other intensively cultivated areas (Nixon et al. 1991), where the condensed areas of summer relative to winter home ranges were likely because of abundant cover and nutritious food throughout the landscape provided by farming activities.

Home-range sizes of deer are variable (Nicholson et al. 1997). Previous reports of home ranges of northern white-tailed deer include estimates of 1.6–4.8 km^2 (Rongstad and Tester 1969); 2.5 km^2 (Sparrowe and Springer 1970); 1.7–4.7 km^2 (Kohn and Mooty 1971); 0.5–4.1 km^2 (Hoskinson and Mech 1976); 0.3–1.4 km^2 (Simon 1986); 1.7 km^2 (VerCauteren and Hygnstrom 1998); and 4.4 km^2 (Kernohan et al. 2002). In general, home-range estimates should be interpreted with caution. Home range can vary with age, sex, habitat, and season (Demarais et al. 2000) and is also affected by human activities (e.g., agricultural). VerCauteren and Hygnstrom (1998) reported that deer in Nebraska shifted their range 174 m toward cornfields when corn development reached tasseling-silking stage, and home range shifted 157 m again after harvest with mean size becoming 32% larger.

MANAGEMENT IMPLICATIONS

In addition to dispersal potentially causing a significant exchange of individuals across management areas (Rosenberry et al. 1999), many of the migratory deer we monitored had summer and winter ranges in different management areas. Because of these results, we recommend that managers consider conducting population surveys during summer and winter. During winters with variable snow depths and temperatures, managers can expect significant movements across management boundaries, especially if critical winter habitat is disproportionately distributed among management units. During milder winters, however, managers can expect deer to make several trips between seasonal ranges or remain on summer range through the winter season. Furthermore, considering home-range sizes during winter were approximately double that of home-range sizes during summer, managers should keep in mind that deer densities may fluctuate spatially and temporally in intensive agricultural areas.

Incorporating predicted emigration and immigration rates into deer population models would improve management strategies. While our data provide estimates of emigration from management areas, these estimates are site-specific. Thus, additional data will be needed to predict movements based on the various habitats and winter severities that characterize deer populations in northern latitudes. Monitoring animals traveling over long distances and measuring movements from unknown locations is difficult (Rosenberry et al. 1999). Use of Global Positioning System (GPS) collars may remedy this problem in the future, but budgetary restraints can limit GPS use. Therefore, we recommend that those quantifying movements of deer intensify monitoring during dispersal and migration periods to strengthen evaluation of deer movement stimuli and timing, and to minimize the loss of signals due to long distance movements.

Although we determined that migration occurred after the firearms hunting season (when deer populations were actively managed), our results indicated that an early onset of severe winter weather could cause migration to occur before hunting seasons, disproportionately affecting deer numbers in management areas serving primarily as winter ranges. Therefore, we recommend that wildlife managers consider timing of winter arrival and severity of winter weather when estimating harvest rates for management units.

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