

# Seasonal movements and home ranges of white-tailed deer in north-central South Dakota

T.W. Grovenburg, J.A. Jenks, R.W. Klaver, C.C. Swanson, C.N. Jacques, and D. Today

**Abstract:** Knowledge of movement patterns of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) inhabiting landscapes intensively modified by agricultural systems is important to the present and future understanding of deer ecology. Little information exists regarding daily and seasonal movements of white-tailed deer in north-central South Dakota. Therefore, our goal was to determine movement patterns and home-range use of female white-tailed deer in north-central South Dakota. From January 2005 to January 2007, 29 adult (>18 months) and 13 yearling (8–18 months) white-tailed deer were monitored for movement using radiotelemetry. We collected 2822 locations, calculated 76 home ranges, and documented 50 seasonal movements. Mean migration distance between summer and winter home ranges was 19.4 km (SE = 2.0 km). Mean 95% home-range size was 10.2 km<sup>2</sup> (SE = 1.2 km<sup>2</sup>,  $n = 27$ ) during winter and 9.2 km<sup>2</sup> (SE = 1.0 km<sup>2</sup>,  $n = 49$ ) during summer. Ambient temperature appeared to be a primary cause of seasonal migration. Additionally, movements exhibited by white-tailed deer in north-central South Dakota were influenced by a highly fragmented landscape dominated by row crops and pasture or grassland.

**Résumé :** Pour comprendre l'écologie actuelle et future du cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)), il est important de connaître les patrons de déplacement des cerfs qui vivent dans les paysages fortement modifiés par les systèmes agricoles. Il existe peu de renseignements sur les déplacements journaliers et saisonniers des cerfs de Virginie dans le centre nord du Dakota du Sud. Notre objectif est donc de déterminer les patrons de déplacement et l'utilisation de l'aire vitale des femelles du cerf de Virginie dans le centre nord du Dakota du Sud. De janvier 2005 à janvier 2007, nous avons suivi par radiotélémetrie les déplacements de 29 adultes (>18 mois) et de 13 jeunes de l'année (8–18 mois) du cerf de Virginie. Nous avons enregistré 2822 repérages, calculé 76 aires vitales et mesuré 50 déplacements saisonniers. La distance moyenne de migration entre les aires vitales d'été et d'hiver est de 19,4 km (ET = 2,0 km). La taille moyenne (à un niveau de 95 %) de l'aire vitale est de 10,2 km<sup>2</sup> (ET = 1,2 km<sup>2</sup>,  $n = 27$ ) en hiver et de 9,2 km<sup>2</sup> (ET = 1,0 km<sup>2</sup>,  $n = 49$ ) durant l'été. La température ambiante semble être la cause principale de la migration saisonnière. De plus, les déplacements faits par les cerfs de Virginie du centre nord du Dakota du Sud sont influencés par le paysage fortement fragmenté et dominé par des cultures en lignes et des pâturages ou prairies.

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## Introduction

Seasonal movement patterns of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) inhabiting Midwest agricultural areas generally include short-distance movements, dispersal movements, and migration (Kernohan et al. 1994; Brinkman et al. 2005). Short-distance movements (which do not involve significant changes in home-range boundaries) are usually related to food availability and occur in regions where seasonal weather changes are mild (Nelson 1998; Sabine et al. 2002).

Seasonal migration between summer and winter ranges typically occurs in populations of white-tailed deer in northern latitudes, and is often associated with variable winter weather conditions (Kernohan et al. 1994; Nelson 1995,

1998; Van Deelen et al. 1998). Mixed migration strategies have been well documented among white-tailed deer in northern latitudes (Sparrowe and Springer 1970; Drolet 1976; Nelson 1995; Sabine et al. 2002; Brinkman et al. 2005). Deer typically migrate a single time for the duration of winter (i.e., obligate migration; Sabine et al. 2002). However, during less severe winter weather patterns, northern white-tailed deer may respond by temporarily shifting habitat use within ranges (i.e., resident) or migrating temporarily (i.e., conditional migration) rather than for the duration of the season (Nelson 1995; Sabine et al. 2002; Brinkman et al. 2005). Extreme variation in yearly snow depth has been hypothesized as a primary cause of mixed migration patterns within populations of white-tailed deer (Sabine et al. 2002).

In the Northern Great Plains, migration from summer to

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winter range is influenced by cold temperatures, seasonal fluctuation, and depth of snow (Nelson 1995, 1998), changing temperatures (Verme 1973), photoperiod, and change in vegetation use associated with snow accumulation and change in temperature (Nelson 1995; Nicholson et al. 1997). White-tailed deer in the Northern Great Plains generally depart for winter range during November and December (Brinkman et al. 2005; Burris 2005; Swanson 2005). Onset of spring migration may be initiated by rising temperatures and decreasing snow cover (Nelson and Mech 1981), and is a release from a restricted food supply to newly available spring forage (Marchinton and Hirth 1984). Spring migration generally occurs during March and April in the Northern Great Plains (Brinkman et al. 2005; Burris 2005; Swanson 2005).

White-tailed deer move through suitable habitat and exhibit relatively high fidelity to seasonal home ranges (Tierson et al. 1985). Migration behavior is thought to be inherited through matriarchal group association, with fawns accompanying dams during migration to winter ranges (Nelson 1994, 1998). Hawkins and Klimstra (1970) documented that female yearlings associated with matriarchs until at least 3 years of age. Migration behavior can differ among individuals within a deer population, and migratory and nonmigratory deer can inhabit the same seasonal range (Nelson and Mech 1992; Van Deelen et al. 1998; Sabine et al. 2002). In eastern South Dakota, migration between summer and winter ranges is generally directed along ecoregion landscape features (Sparrowe and Springer 1970; Kernohan et al. 1994; Burris 2005).

Movements of white-tailed deer in eastern South Dakota and western Minnesota are well documented. For instance, Kernohan et al. (1994) noted that seasonal movements between winter and summer ranges exceeded 10 km, while Brinkman et al. (2005), Burris (2005), and Swanson (2005) documented mean migration distances of 10.1, 10.1, and 14.6 km, respectively, in Midwestern deer populations. Nevertheless, limited information exists on timing and extent of movement of white-tailed deer relative to ecoregions in the Northern Great Plains. Because vegetation and climatic characteristics are more similar within than across ecoregions, we hypothesized that deer would exhibit fidelity to their natal region and consequently structure movements to enhance survival and long-term fitness. Furthermore, in highly fragmented habitats, white-tailed deer are often forced to disperse long distances before finding suitable habitat (Long et al. 2005). Thus, our objectives were to determine seasonal movement patterns and home ranges of white-tailed deer in north-central South Dakota. We hypothesized that owing to effects of snow depth and low ambient temperatures, migration behavior would be similar to that of deer occupying northern latitudes. Additionally, we hypothesized that migration distances would be greater than those documented in the northern Midwest agricultural region because of limited patches of permanent cover (i.e., trees).

## Materials and methods

We conducted our study from January 2005 to January 2007 in north-central South Dakota (45°N–46°N, 98°W–

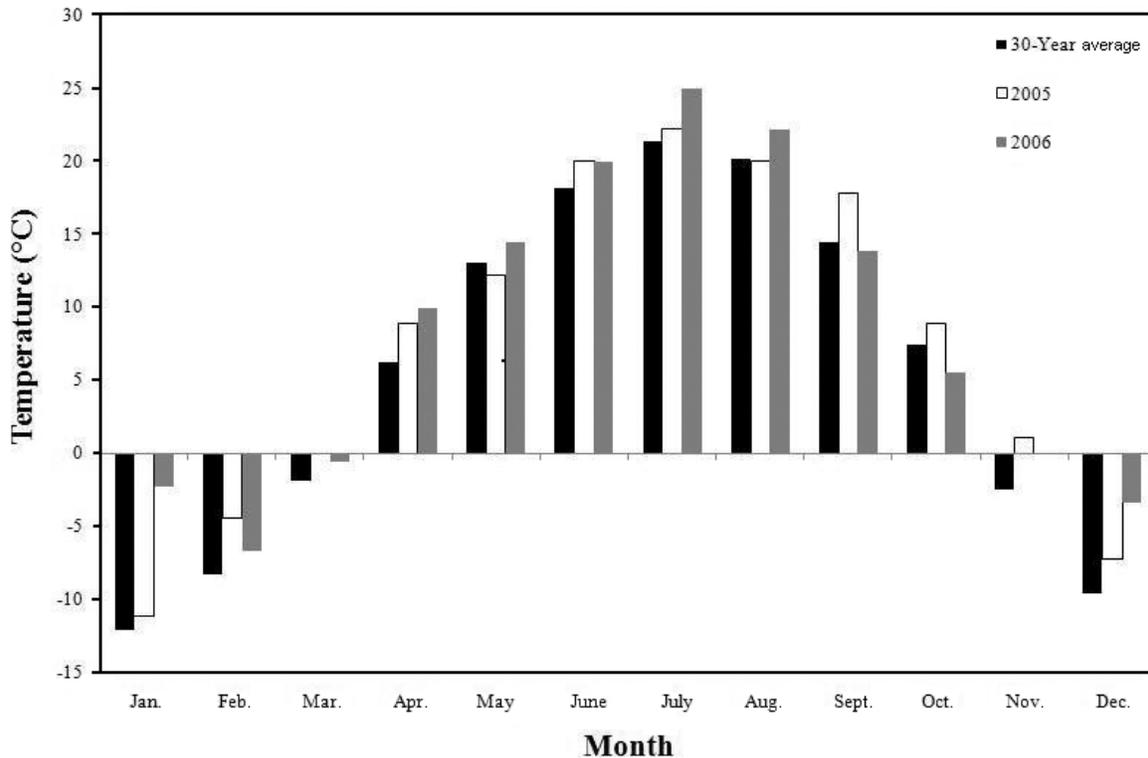
100°W), which included Brown, Edmunds, Faulk, and McPherson counties. Mean annual (30-year average) precipitation was 49.5 cm, and during 2005 and 2006 was 45.5 and 31.9 cm, respectively. Mean summer and winter (30-year average) temperatures ranged from 18.2 to 21.3 °C and –8.3 to –12.1 °C, respectively. During 2005 and 2006, 10 (83.3%) and 9 (75.0%) months were warmer than the 30-year average (Fig. 1; South Dakota Office of Climatology 2009). The area was located within the Northwestern Glaciated Plains and the Northern Glaciated Plains level III ecoregions (Bryce et al. 1998). The landscape is flat to gently rolling terrain intermixed with numerous pothole wetlands and mounds of glacial till (Bryce et al. 1998). We selected study sites because they served as traditional winter ranges for white-tailed deer.

Important habitats of white-tailed deer occupying the Northern Great Plains consist of draws, swales, and lowlands that receive greater moisture than surrounding areas, and river floodplains (Petersen 1984). Although marshes and sloughs occupy a relatively small proportion of the Northern Great Plains and our study area (10.4% of the land area; Smith et al. 2002), they provide critical cover and foraging areas for white-tailed deer throughout north-central South Dakota (Petersen 1984). Land use in the region was dominated by agriculture, with cultivated land and grassland constituting 42.4% and 44.6%, respectively, of total land use; mean forest cover was 2.3% (Smith et al. 2002). The four-county area had 71 896 ha of planted grasslands enrolled in the 2004 Conservation Reserve Program (CRP; South Dakota Agriculture Statistics Service 2007).

We captured adult female white-tailed deer from January to April 2005 and January 2006 using modified Clover traps (Clover 1956), helicopter net guns (Jacques et al. 2009), and immobilizing drugs (4.4 mg/kg Telezol™ and 2.2 mg/kg Xylazine™) delivered via a Pneu-Dart (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) with flight stabilizers from a Dan-Inject CO<sub>2</sub> rifle, model JM Standard (Dan-Inject of North America, Ft. Collins, Colorado, USA; Haulton et al. 2001); we administered Yohimbine™ (0.2 mg/kg) intravenously as an antagonist. We fitted ear tags and radiocollars (Advanced Telemetry System, Isanti, Minnesota, USA) to each captured deer; radio collars were equipped with a mortality sensor that switched to mortality mode after the transmitter remained stationary for ≥8 h. All methods used in this research were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 04-A009).

We monitored radio-collared deer for mortality, subsequently located them 2–3 times/week through January 2007, and monitored them for movement through spring 2007. We used ground triangulation using a null-peak antenna system (Brinkman et al. 2002) to obtain location estimates. Three to five directional bearings were obtained from established telemetry stations using an electronic digital compass (C100 Compass Engine, KVH Industries, Inc., Middletown, Rhode Island, USA; Cox et al. 2002). Estimated azimuth accuracy was ±1°. We estimated locations using LOCATE III (Nams 2006) using a minimum of three azimuths for all deer locations. We excluded locations with 95% error ellipses ≥20 ha from seasonal movement and home-range analyses (Brinkman et al. 2005). We never tracked animals on suc-

**Fig. 1.** Mean monthly temperatures including the 30-year average for the study area inhabited by white-tailed deer (*Odocoileus virginianus*) in north-central South Dakota, 2005–2006 (South Dakota Office of Climatology 2009).



cessive days or at successive times during the day to maintain temporal and spatial independence of observations for home-range estimates (McNay et al. 1994).

We used ArcView (Environmental Systems Research Institute, Inc., Redlands, California, USA) to assess seasonal movements relative to physiographic regions. We used the fixed kernel method using the Home Range Extension (HRE) for ArcView (Rodgers and Carr 1998) to calculate 50% and 95% seasonal home ranges. We applied least-squares cross-validation (LSCV; Seaman et al. 1999) to estimate the smoothing parameter.

We classified deer as migrants if no overlap existed between seasonal home ranges (Brinkman et al. 2005). We calculated migration distance using straight-line distance between harmonic centers of seasonal locations. We calculated date of migration as the mean date between consecutive locations on separate seasonal ranges (Nelson 1995). We classified deer as dispersers if they moved from original home ranges and established permanent home ranges elsewhere (Nelson and Mech 1992; Kernohan et al. 1994; Brinkman et al. 2005). We classified individuals as obligate migrators if they made a single movement to winter ranges and subsequently remained there until returning (during spring) to previous summer ranges (Sabine et al. 2002; Brinkman et al. 2005). We classified animals as facultative or conditional migrators (Nelson 1995; Nicholson et al. 1997; Sabine et al. 2002) if they failed to migrate during any documented migration period or if they made several trips to a seasonal home range for <1 month (Nelson 1995). We classified deer as residents if seasonal home ranges overlapped or animals failed to migrate for  $\geq 3$  consecutive migration periods (VerCauteren and Hygnstrom 1998). We

defined spring migration as travel from winter to summer range, and fall migration as travel from summer to winter range (Brinkman et al. 2005).

We calculated deer winter severity indices (DWSI; Brinkman et al. 2005) for winter 2004–2005 and 2005–2006 to determine whether temperature and snow depth influenced migration. For every day that mean temperature was  $\leq -7$  °C, one point was accumulated, with an additional one point for each day snow depth was  $\geq 35.0$  cm (Brinkman et al. 2005) during the months of November–March (South Dakota Office of Climatology 2009).

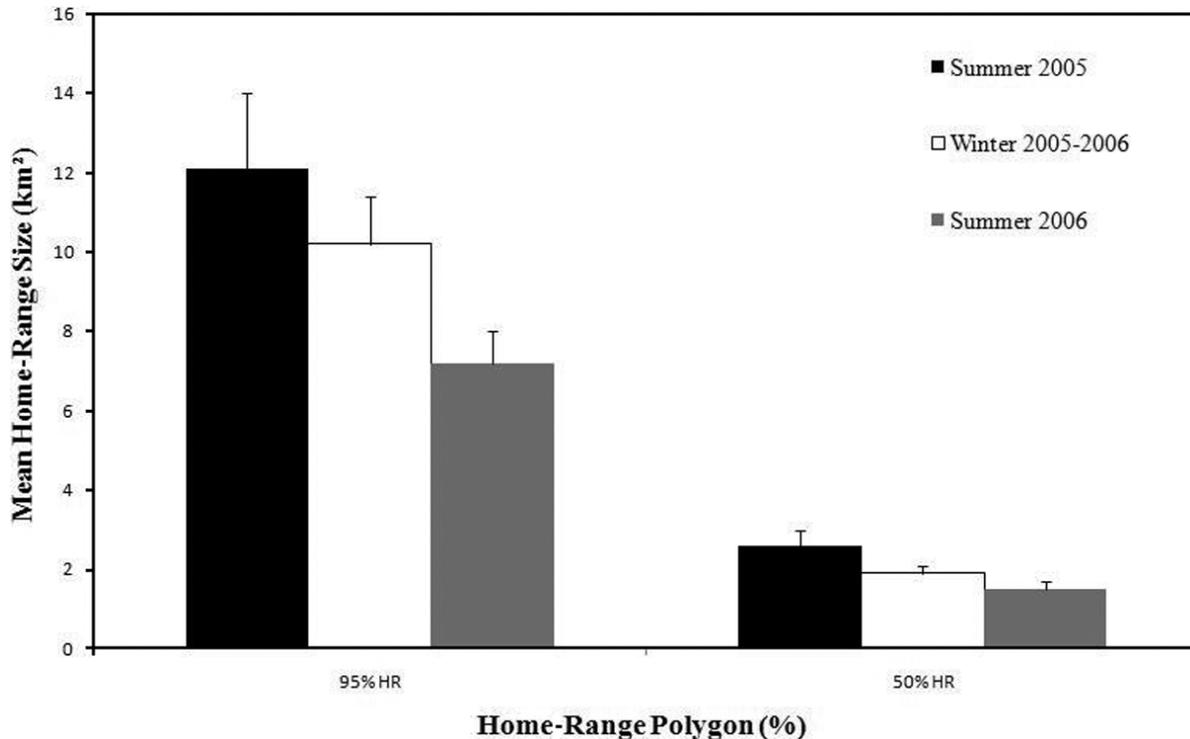
We used SAS version 9.1 (SAS Institute Inc. 2000) to conduct statistical analyses. We used analysis of variance (ANOVA) and pairwise comparisons to compare home-range sizes and migration distances by year and season.

## Results

Forty-two adult and yearling female white-tailed deer were captured and radio-collared during January–April 2005 ( $n = 22$ ) and January 2006 ( $n = 20$ ). We collected 2822 animal locations, with a mean 95% error ellipse of 6.6 ha. We documented 50 seasonal movements during four migratory periods: spring 2005 ( $n = 6$ ), fall 2005 ( $n = 8$ ), spring 2006 ( $n = 20$ ), and fall 2006 ( $n = 16$ ). Seventy-six individual seasonal home ranges were calculated during three periods: summer 2005 ( $n = 20$ ), winter 2005–2006 ( $n = 27$ ), summer 2006 ( $n = 29$ ).

We documented movement for 26 of 42 (61.9%) female white-tailed deer; 23 (59.0%) initiated seasonal migration and 3 (7.1%; 2 yearlings, 1 adult) dispersed a mean distance of 59.9 km (SE = 11.9 km, range = 36.2 km). Overall

**Fig. 2.** Mean seasonal home range size for adult white-tailed deer (*Odocoileus virginianus*) in north-central South Dakota, 2005–2006. Summer 2005 home-range estimates were calculated from data obtained from 21 individuals. Winter 2005–2006 home-range estimates were calculated from data obtained from 32 individuals. Summer 2006 home-range estimates were calculated from data obtained from 30 individuals.



**Table 1.** Mean migration distance, standard error, number of animals migrating, and median date of migration during four migratory periods for white-tailed deer (*Odocoileus virginianus*) in north-central South Dakota, 2005–2006.

Migratory period	Distance (km)			Date
	Mean	SE	<i>n</i>	
Spring 2005	34.8	11.0	6	25 Apr.
Fall 2005	15.9	3.8	8	18 Nov.
Spring 2006	18.9	2.8	20	12 Apr.
Fall 2006	19.1	3.3	16	27 Nov.

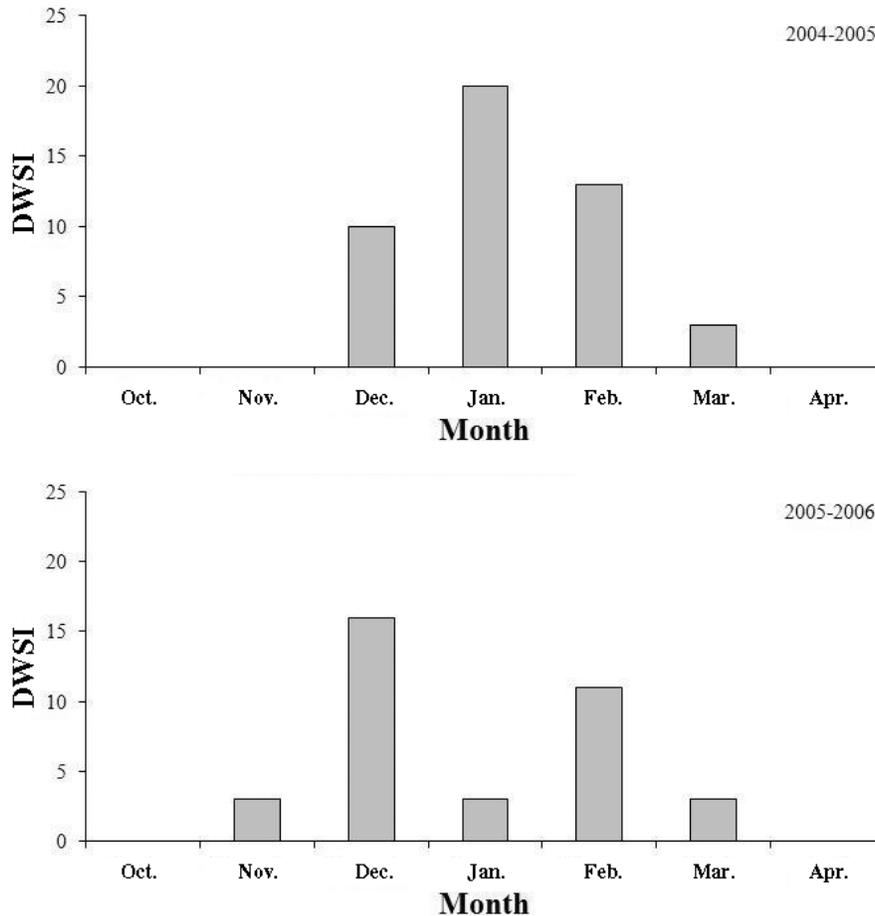
(2005–2006) mean migration distance (19.4 km, SE = 2.0 km,  $n = 50$ ; Table 1) of deer was similar between years ( $F_{[1,49]} = 0.15$ ,  $P = 0.704$ ) and seasons ( $F_{[1,49]} = 0.49$ ,  $P = 0.488$ ). Mean spring migration direction was  $294.3^\circ$  (SE =  $12.2^\circ$ ,  $n = 26$ ) and did not differ between years ( $t_{[24]} = 0.43$ ,  $P = 0.672$ ). Of 34 female white-tailed deer monitored  $\geq 3$  consecutive migratory periods, 16 (47.1%) were obligate migrators, 5 (14.7%) were conditional migrators, and 13 (38.2%) were residents. Mean obligate and conditional migration distances were 22.2 km (SE = 2.2 km,  $n = 40$ ) and 6.6 km (SE = 0.7 km,  $n = 7$ ), respectively.

Percentage of migratory deer crossing ecoregions during seasonal movement ranged from 60.0% to 81.3%. Median migration dates for animals crossing ecoregion boundaries were comparable to median migration dates for all migratory deer during this study. Fourteen (87.5%) obligate and four (80.0%) conditional migrants crossed ecoregion boundaries.

We calculated individual home ranges using a minimum of 30 and a mean of 35.1 (SE = 0.5,  $n = 76$ ) locations. Because of capture operations that continued for  $>3$  months,  $<30$  locations/animal was collected on radio-collared deer during winter 2004–2005, prohibiting calculation of seasonal home ranges. Mean 95% ( $F_{[2,73]} = 3.67$ ,  $P = 0.030$ ) and 50% ( $F_{[2,73]} = 4.19$ ,  $P = 0.019$ ) home ranges differed among seasons (Fig. 2). Mean 95% ( $t_{[74]} = 0.76$ ,  $P = 0.450$ ) home ranges were similar between adults (9.2 km<sup>2</sup>, SE = 0.9 km<sup>2</sup>,  $n = 56$ ) and yearlings (10.5 km<sup>2</sup>, SE = 1.7 km<sup>2</sup>,  $n = 20$ ). Mean 50% ( $t_{[74]} = 0.86$ ,  $P = 0.392$ ) home ranges were similar between adults (1.9 km<sup>2</sup>, SE = 0.2 km<sup>2</sup>,  $n = 56$ ) and yearlings (2.2 km<sup>2</sup>, SE = 0.4 km<sup>2</sup>,  $n = 20$ ).

Mean DWSI during winter 2004–2005 and 2005–2006 was 46.0 and 36.0 (Fig. 3), respectively, and fall migration coincided with decreasing temperatures (Fig. 4). During fall 2005, movement of all migratory deer occurred 18–21 November following a change in temperature. Mean ambient temperatures during 15–17 November were  $-4$  to  $-10^\circ\text{C}$  and were the lowest recorded up to that date. During fall 2006, 3 of 16 (18.8%) deer with known departure dates initiated migration during 31 October – 3 November in response to declining ambient temperatures. Ambient temperatures during this period were  $-3$  to  $-6^\circ\text{C}$ , and consequently, were the lowest recorded temperatures through 3 November 2006. Interestingly, fall migration was not documented from 4 to 13 November when recorded temperatures reached a high of  $11^\circ\text{C}$ . From 14 to 29 November, 10 (62.5%) additional deer initiated fall migration as ambient

**Fig. 3.** Monthly white-tailed deer (*Odocoileus virginianus*) winter severity indices (DWSI) for study site in north-central South Dakota (one point accumulated for each day ambient temperature  $\leq -7$  °C, and an additional point accumulated for each day with snow depths  $\geq 35.0$  cm; South Dakota Office of Climatology 2009).



temperatures decreased to  $-16$  °C (Fig. 4). Snow depth was not a factor in initiating fall migration (Fig. 4).

Spring migration also coincided with changes in ambient temperature (Fig. 5). During spring 2005, 3 of 6 (50%) deer with known departure dates initiated migration during 4–15 April, when mean ambient temperatures were 8–16 °C. Remaining deer initiated migration during 6–10 May when mean ambient temperatures were 12–22 °C. During spring 2006, only 6 of 23 (26.1%) deer with known departure dates initiated migration prior to 6 April. Ambient temperatures during 1 January – 6 April were  $-22$  to 14 °C. From 7 to 12 April, 12 of 23 (52.2%) deer initiated migration following 10 days when temperatures were 2–14 °C. The remaining 5 (21.7%) deer initiated migration 26 April – 31 May when temperatures were 4–24 °C. Snow depth was not a factor in initiating spring migration (Fig. 5).

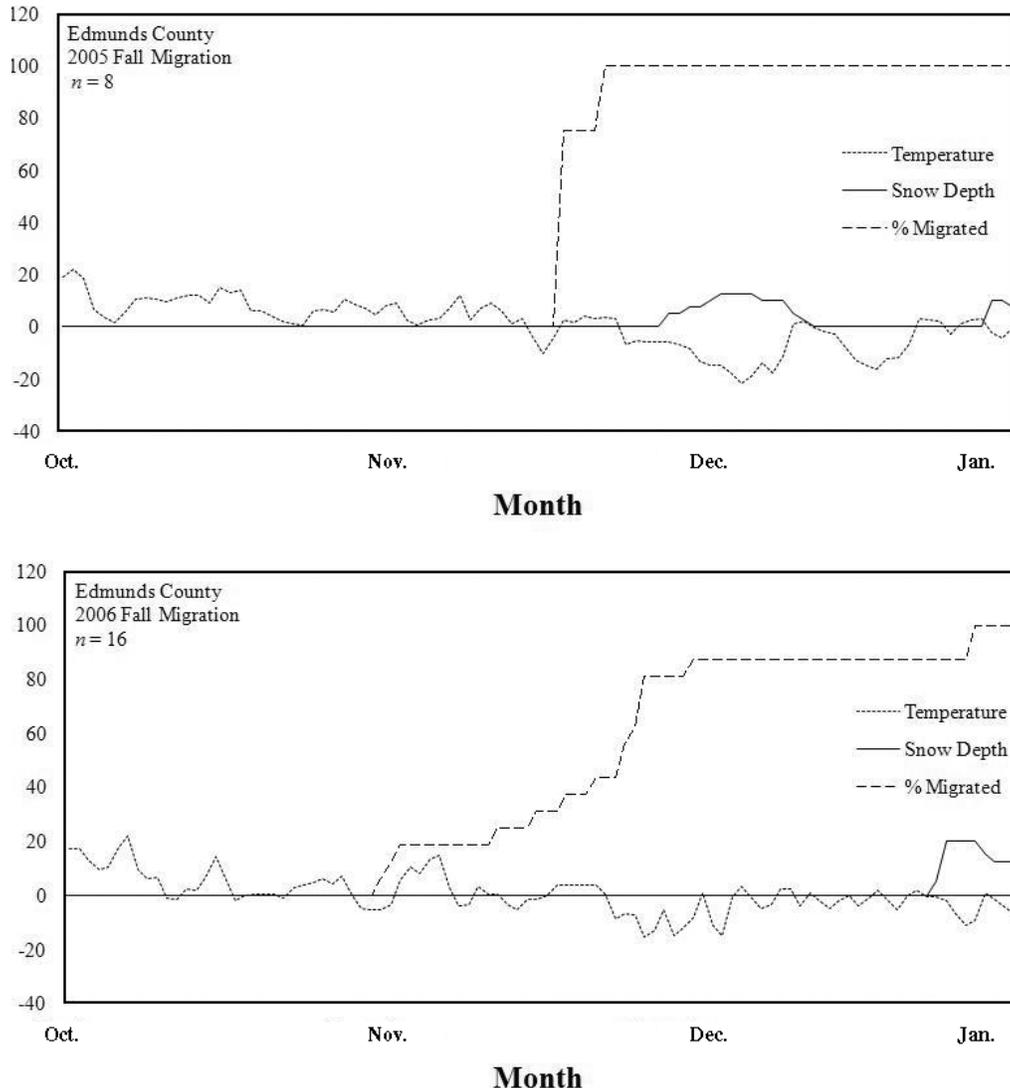
## Discussion

Mean migration distance (19.4 km) of female white-tailed deer in north-central South Dakota was greater than previously documented in eastern South Dakota (10.1 km: Burris 2005) and Minnesota (10.1 km: Brinkman et al. 2005; 14.6 km: Swanson 2005), but was similar to those reported for other northern populations of white-tailed deer

(23.2 km: Sparrowe and Springer 1970; 13.8 km: Verme 1973; 17.0 km: Nelson and Mech 1981; 15.7 km: Sabine et al. 2002). A possible factor influencing longer migration distances in north-central South Dakota may have been limited forest cover. While white-tailed deer are habitat generalists, forest cover is important and provides thermal cover, escape shelter, and food resources (Harlow 1984; Long et al. 2005). In landscapes with limited tree cover, deer likely travel greater distances to occupy suitable habitat patches (Long et al. 2005).

White-tailed deer in north-central South Dakota exhibited a mixture of movement strategies consisting of permanent residents, conditional migrators, obligate migrators, and dispersers; our results indicated that white-tailed deer populations were composed largely of permanent residents and obligate migrators. Interestingly, percentage of conditional migration documented during our study was substantially lower than in other regional studies. For instance, Brinkman et al. (2005) and Swanson (2005) reported 35% and 28% conditional migration rates, respectively, throughout southern Minnesota. Similarly, Burris (2005) classified 36% of study populations as conditional migrators. Differences in deer movement strategies between our study and previous investigations may be partly associated with regional variation in winter severity. For instance, Brinkman et al. (2005)

**Fig. 4.** Fall migration for radio-collared white-tailed deer (*Odocoileus virginianus*) in north-central South Dakota. The y axis is shared by all three variables (i.e., temperature (°C), snow depth (cm), migratory deer (%)). A migration event represents the cumulative percentage of migrating individuals with known departure dates from summer range.



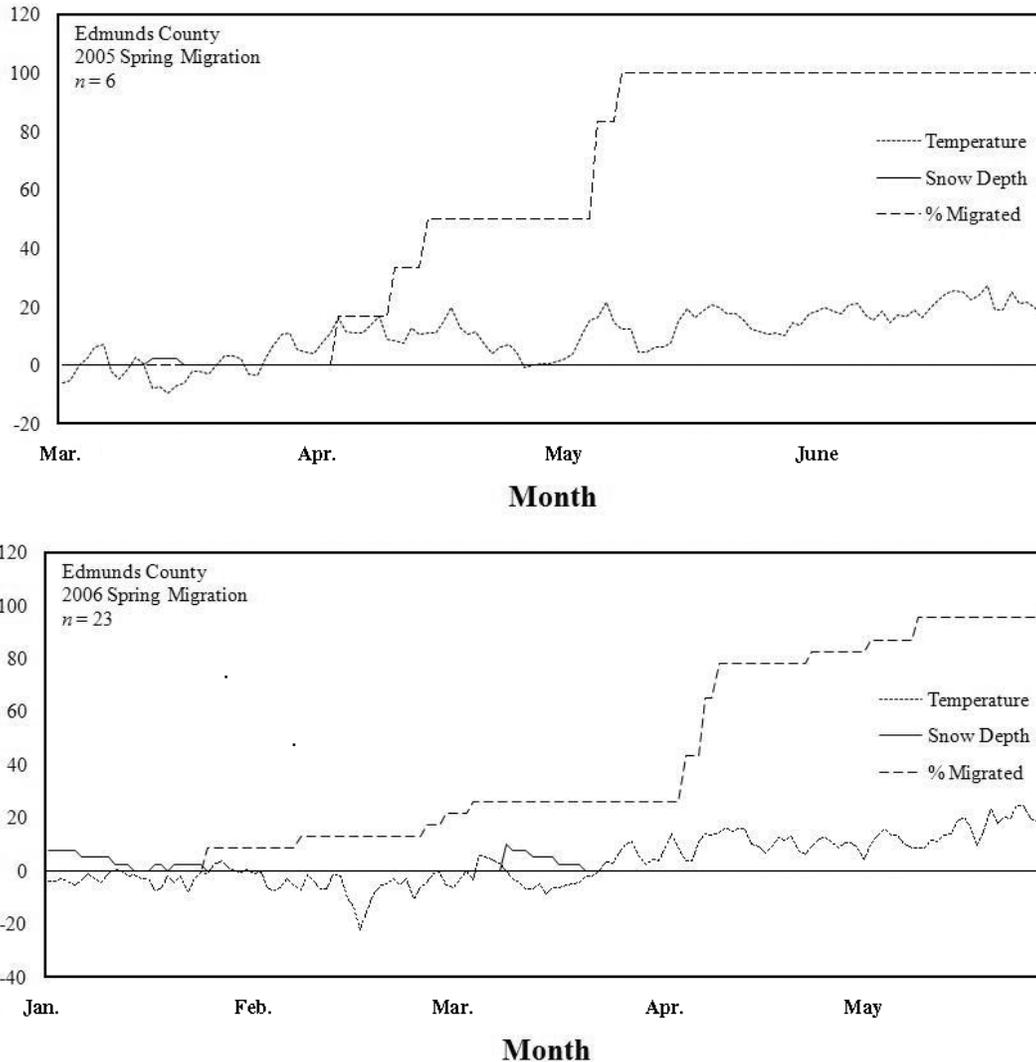
concluded that increasingly severe winters exerted the strongest effect on seasonal migration and migration strategy in northern populations of white-tailed deer. Similarly, Nicholson et al. (1997) documented that mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) exhibited a mixed migration strategy in areas with variable precipitation and snow cover.

We documented a higher percentage of obligate migrators during our study than in other regional studies. For instance, Brinkman et al. (2005) and Swanson (2005) reported 42.5% and 27.8% obligate migration rates, respectively, throughout southern Minnesota. Similarly, Burris (2005) reported 40.0% of study populations as obligate migrators. Additionally, we documented longer migration distances for obligate migrators during our study. Burris (2005) and Swanson (2005) documented 11.8 and 15.9 km mean obligate migration distances, respectively. Fieberg et al. (2008) noted that the proportion of deer classified as obligate migrators was inversely related to the number of years individuals were monitored owing to varying winter severity. Animals classified as obli-

gate migrators during severe winter weather transitioned to conditional migrators during mild winters (Fieberg et al. 2008). However, this was counter to our classification of a high percentage of obligate migrators during consecutive mild winters when we would have expected animals to become conditional migrators. Limited permanent cover (i.e., forested cover; Smith et al. 2002) in the study area may have contributed to migratory movements during relatively mild winters.

White-tailed deer in north-central South Dakota exhibited significant movement across ecoregion boundaries during migratory events; direction of migration was west-northwest for 84.6% of all spring movements. One explanation for this behavior was that animals displayed a learned migration pattern (Nelson 1998). Migration was reported to be strongly influenced by learning and mimicry; deer exhibited memory for compass bearing and distance and kept original migration patterns learned from their dam (Nelson 1998). Moreover, Nelson (1998) documented a proclivity to use

**Fig. 5.** Spring migration and dispersal for radiocollared white-tailed deer (*Odocoileus virginianus*) in north-central South Dakota. The y axis is shared by all three variables (i.e., temperature (°C), snow depth (cm), migratory deer (%)). A migration event represents the cumulative percentage of migrating individuals with known departure dates from winter range.



migration memory independently of topography and habitat. Site fidelity also could have influenced movements across ecoregion boundaries that were documented during our study. Site fidelity has been well documented in many ungulates including white-tailed deer (Tierson et al. 1985; Kernohan et al. 2002). Tierson et al. (1985) documented significant fidelity to a specific summer range, whereas Kernohan et al. (2002) reported moderate site fidelity between years and seasons.

Causes of dispersal in white-tailed deer have included inbreeding avoidance and mate competition and ultimate causes are elicited by different social cues that are season specific (Long et al. 2008). Dispersal rates for female white-tailed deer documented during our study (7.1%) were similar to those documented in western Minnesota (8.0%: Brinkman et al. 2005) and eastern South Dakota (6.2%: Burris 2005). Long dispersal distances documented during our study may have been an attempt to locate unoccupied suitable habitat. In intensive agricultural areas with limited cover that can change annually owing to crop rotation pat-

terns, deer often travel long distances before locating suitable cover (Demarais et al. 2000; Nixon et al. 2001; Brinkman et al. 2005).

Previous research on white-tailed deer indicated that onset of cold ambient temperatures and depth of snow were primary influences on seasonal movement from summer to winter ranges (Verme 1973; Nelson 1995; Brinkman et al. 2005). Tierson et al. (1985) and Nelson (1995) reported a temperature threshold of  $-7^{\circ}\text{C}$  as initiating migration. In our study, temperature was a primary influence on seasonal deer movement in north-central South Dakota. In contrast, snow depth was not a primary factor in initiating spring or fall migrations. In fact, maximum snow depth during our study exceeded 13.0 cm (20.3 cm on 30 December 2006) on only one occasion and was below documented migration thresholds of 30.4 cm (Drolet 1976), 35–40 cm (Nelson and Mech 1981), and 40 cm (Sabine et al. 2002).

Median fall migration dates during our study were similar to 28 November – 28 December (Nelson 1995), 8 December (Van Deelen et al. 1998), 7 December – 12 February (Sa-

bine et al. 2002), 28 November (Brinkman et al. 2005), 28–29 November (Burris 2005), and 24–26 November (Swanson 2005). Fall migration was initiated when temperatures were  $<0^{\circ}\text{C}$  for  $>3$  days and slowed or was interrupted by increasing ( $>0^{\circ}\text{C}$ ) ambient temperatures. Migration continued when temperatures decreased to  $<0^{\circ}\text{C}$ , and all migration was completed, regardless of distance traveled, when ambient temperatures were maintained at  $<0^{\circ}\text{C}$  for  $\geq 3$  weeks. Movement through deep snow is metabolically expensive because animals must expend energy to elevate the body repeatedly, and this metabolic cost of movement increases curvilinearly with snow depth (Parker et al. 1984; Robbins 2001). Additionally, heat loss may exceed energy expenditure for standard metabolism and activity when temperatures are  $\leq -7^{\circ}\text{C}$  (DelGuidice 2000). Because of these costs, it would be beneficial for deer to migrate prior to snow accumulation if environmental variables (i.e., ambient temperature, snow depth) or past experience were sufficient to predict winter severity (Fieberg et al. 2008). Moreover, shallow snow depths ( $<20.3$  cm) during our study would have imposed minimal energy costs relative to deer movements (Moen 1968, 1976; Fieberg et al. 2008). Thus, temperatures  $<0^{\circ}\text{C}$  for  $>3$  days likely represent a primary cue initiating fall migration.

Median spring migration dates were similar to 19 March – 4 May (Nelson 1995), 4 April (Van Deelen et al. 1998), 11 March – 29 April (Sabine et al. 2002), 8–18 April (Brinkman et al. 2005), 24–25 March (Burris 2005), and 6–22 April (Swanson 2005). Spring migration was initiated when ambient temperatures exceeded  $0^{\circ}\text{C}$  for several ( $\geq 3$ ) days and would slow or stop when temperatures decreased below  $0^{\circ}\text{C}$ . Interestingly, migration was reinitiated when ambient temperatures again exceeded  $0^{\circ}\text{C}$ . While Nelson (1995) documented snow cover as a primary influence on spring migration, snow cover had little impact on spring migration by deer in north-central South Dakota throughout our study. Spring migration in this region may have been in response to increased metabolic demands. Photoperiod is known to regulate voluntary food intake (VFI) cycles of deer (Brown et al. 1979), and under normal conditions, peak VFI occurs in mid-summer (Loudon et al. 1989; Loudon 1994). This peak in VFI cycle matches energy requirements for peak lactation in females (Loudon 1994). Beier and McCullough (1990) observed an increase in spring activity in female white-tailed deer that was consistent with a rise in metabolic demand owing to late pregnancy. In this region, parturition occurs from mid-May until mid-June, with peak parturition occurring 25–28 May (Burris 2005; Swanson 2005). In heterogeneous landscapes such as the Northern Great Plains, increased survival and recruitment of fawns may trigger migratory movements to suitable home ranges by female deer, thereby enabling individuals to optimize use of fragmented landscapes (Nixon et al. 2008) and maximize individual fitness.

Variation in seasonal home-range size between summer 2005 and 2006 was notable. Unfortunately, we did not have detailed data on quality and distribution of forage and cover habitats to test for temporal differences in home-range size. Consequently, mechanisms affecting this variation in home-range size were speculative. Smaller home ranges during summer 2006 may have been influenced by sustained

drought conditions. During 2006, the study area had a drought intensity level of severe to extreme (National Drought Mitigation Center 2007) with moisture levels 35.5% below the 30-year average. We suggest additive effects of drought conditions during 2006 and limited distribution of water resources throughout north-central South Dakota may have contributed, in part, to temporal differences in daily movements and home-range use by white-tailed deer in our study area.

Our findings illustrate the complexities of identifying ultimate factors initiating migration in white-tailed deer. While snow depth has been documented as the primary factor influencing the initiation of seasonal migration in several studies (Nelson 1995, 1998; Brinkman et al. 2005), our research indicated that snow had minimal impact on initiation of migration. Additionally, differences in obligate and conditional migration rates documented between our study and recent work (Brinkman et al. 2005; Fieberg et al. 2008) suggest the need for further studies to determine the relationship of additional variables to migratory strategies. Of particular interest are the effects of global warming, landscape metrics, habitat fragmentation, population density, and patch size on seasonal movement strategies of white-tailed deer occurring in the Northern Great Plains.

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