Influence of landscape characteristics on migration strategies of white-tailed deer

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A trade-off exists for migrating animals as to whether to migrate or remain residents. Few studies have documented relationships between landscape variables and deer migration strategies. From 2000 to 2007 we captured 267 adult female white-tailed deer (*Odocoileus virginianus*) at 7 study sites in Minnesota and South Dakota and monitored 149 individuals through ≥3 seasonal migration periods (585 deer-migration seasons). All deer classified as obligate migrators with ≥3 migrations (range 3–9 migration seasons) maintained their obligate status for the duration of the study. Multinomial logistic odds ratios from generalized estimating equations indicated that the odds of being a resident increased by 1.4 and 1.3 per 1-unit increase in forest patch density and mean area, respectively, compared to migrating deer. Odds of being an obligate migrator increased by 0.7 and 0.8 per 1-unit decrease in forest patch density and mean area, respectively, compared to resident or conditional migrating deer. Areas inhabited by resident deer were characterized by greater number of forest patches per 100 ha and larger mean forest patch area than conditional and obligate migrant areas. Odds of migrating increased by 1.1 per 1-unit increase in deer winter severity index. Migration behavior of white-tailed deer varied among regions, and land-cover and landscape characteristics provided predictive indicators of migration strategies for deer that could have important implications for conservation, metapopulation dynamics, and species management.

Key words: forest cover, landscape, migration strategy, Minnesota, *Odocoileus virginianus*, South Dakota, white-tailed deer

Migration has been defined as seasonal and directional animal movement from one region or climate to another (Irwin 2002), and selection should favor those individuals that migrate if doing so increases their reproductive success (Baker 1978; Nicholson et al. 1997). Therefore, animals free to choose migration strategies and habitats should maximize their reproductive success (Fretwell 1972; Nicholson et al. 1997). However, a trade-off might exist for migrating animals as to whether to migrate or remain residents (Nicholson et al. 1997). For instance, migratory deer might have access to high-

quality habitats and be able to produce more or healthier young, increasing their reproductive success (Nicholson et al. 1997).

Seasonal migration is common among cervids and well documented for North American ungulates, including elk (*Cervus elaphus*—Hebblewhite and Merrill 2007; Irwin 2002),

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caribou (*Rangifer tarandus*—Hemming 1971), mule deer (*Odocoileus hemionus*—Nicholson et al. 1997; Sawyer et al. 2005), pronghorn (*Antilocapra americana*—Jacques et al. 2009a; Sawyer et al. 2005; Yoakum and O'Gara 2000), and white-tailed deer (*O. virginianus*—Brinkman et al. 2005; Grovenburg et al. 2009). Several strategies relating to migration can occur within deer populations because of environmental fluctuations and differences in costs of migration (Fretwell 1972; Nicholson et al. 1997). Northern deer exhibit various migration strategies, including resident (do not migrate) and obligate (migrate a single time for the duration of the season and migrate every season) and conditional (migrating some seasons but not others, or temporarily migrating for <1 month) migration (Brinkman et al. 2005; Fieberg et al. 2008; Nelson 1995; Sabine et al. 2002).

Understanding the relationships between habitat characteristics and migratory strategies of white-tailed deer (*O. virginianus*) is important when studying the spread of disease, population dynamics, and range management. Habitat characteristics affect deer distribution and abundance (Demarais et al. 2000; Roseberry and Woolf 1998; Sinclair 1997) and survivorship (Klaver et al. 2008), and use of forested habitats for thermal cover, escape shelter, and food resources is well documented in the ecological literature (Harlow 1984; Long et al. 2005). Forest cover has been documented as influencing deer behavioral responses (e.g., larger social groups in less forested regions than in heavily forested regions—Hirth 1977; Long et al. 2005), and deer thrive in edge habitats, possibly indicating higher quality habitat for female deer (Rohm et al. 2007). Moreover, more irregular forested patches can affect predator success in locating and capturing prey (Rohm et al. 2007). In regions with minimal forested cover, however, deer can initiate migration to find suitable forest habitat during winter (Grovenburg et al. 2009).

To our knowledge, previous reports describing relationships among landscape and environmental variables and deer movement strategies are limited to a single study. Fieberg et al. (2008) determined that the annual estimated proportion of deer migrating from spring–summer–autumn range to winter range was correlated positively with winter severity, and classification of obligate migrators was related inversely to number of years individual deer were monitored. However, relationships between variability in deer migratory strategies and availability of forested cover are unknown. The objective of our study was to evaluate how forested cover influenced migration classification of white-tailed deer. We used study sites with a continuum of forested cover to test whether the number of forested patches, forested patch size, and amount of forested edge influenced migratory strategies of white-tailed deer. Because of the benefits of forested cover documented in previous studies, we hypothesized that increased forested cover (i.e., greater number of patches, larger patch size, and more irregular-shaped patches) would result in greater numbers of resident deer. Additionally, we evaluated how winter severity influenced initiation of migration by condi-
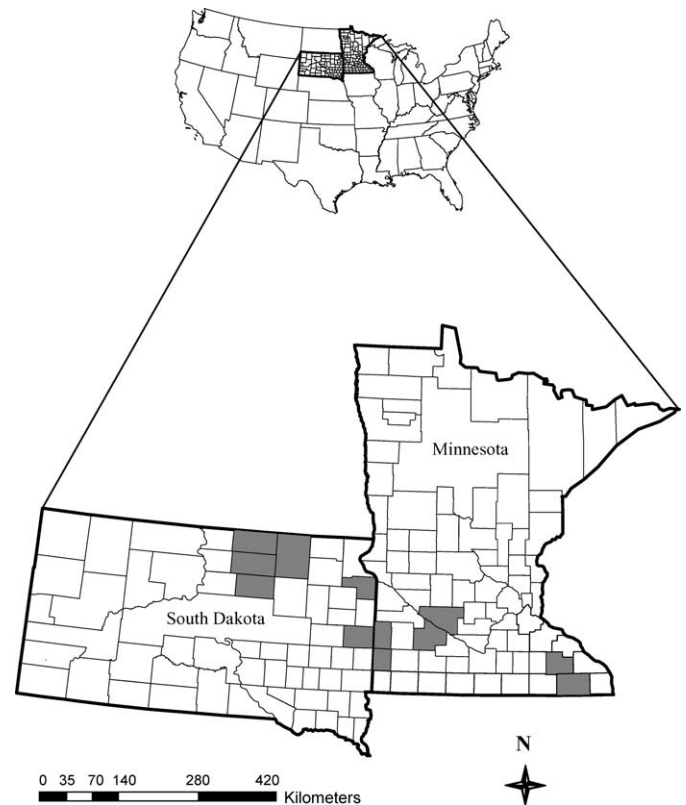

Fig. 1.—White-tailed deer (*Odocoileus virginianus*) study areas in southeastern Minnesota (Fillmore and Olmsted counties), southwestern Minnesota (Lincoln, Pipestone, Renville, and Redwood counties), eastern South Dakota (Brookings and Grant counties), and north-central South Dakota (Brown, Edmunds, Faulk, and McPherson counties), 2000–2007.

tional migrants. Migration between summer and winter ranges in northern latitudes has long been considered an adaptive response to snow depth and cold temperatures (Brinkman et al. 2005; Nelson 1998) and could be a survival strategy for deer (Fieberg et al. 2008). Consequently, we hypothesized that winter severity would influence migration of conditional migrants; odds of a conditional migrant exhibiting migration behavior would increase with increasing winter severity. Evaluation of these hypotheses will contribute to a better understanding of the influence of an increasingly fragmented environment on northern populations of white-tailed deer.

MATERIALS AND METHODS

Study area.—We conducted our study at sites extending approximately 700 km west-to-east from north-central South Dakota (45°56′N, 99°43′W) to southeastern Minnesota (43°30′N, 91°43′W; Fig. 1). Southeastern Minnesota study sites differed from other areas by being characterized by steeply sloped topography and greater percent of forested cover (Table 1). The remaining study areas graduated from one to another; cultivated land increased and grassland–pasture decreased from west-to-east (Minnesota Department of Natural Resources 2009; Smith et al. 2002; Table 1). Mean

TABLE 1.—Land-cover and environmental characteristics for white-tailed deer (*Odocoileus virginianus*) study sites in South Dakota and Minnesota, 2000–2007 (Midwest Regional Climate Center 2009; Minnesota Department of Natural Resources 2009; Smith et al. 2002; South Dakota Office of Climatology 2009).

	North-central South Dakota	Eastern South Dakota	Southwestern Minnesota	Southeastern Minnesota
Forested cover (%)	1.9–2.8	1.6–2.5	1.5–7.3	7.7–20.0
Cultivated land (%)	32.1–56.7	51.7–58.3	81.1–93.4	55.4–62.8
Pasture–grassland (%)	30.6–55.6	31.5–41.8	2.4–14.6	14.2–23.6
Wetland (%)	9.4–11.9	3.5–4.4	0.2–0.4	<0.5
Free water (%)	<0.5	0.8–2.3	0.5–0.9	0.2–0.4
$\bar{X}$ winter temperature (°C)	−9.4	−8.7	−9.8	−6.3
$\bar{X}$ summer temperature (°C)	20.9	21.3	23.1	20.1
$\bar{X}$ annual precipitation (cm)	49.1	55.3	65.4	83.5

annual precipitation increased west-to-east, and mean annual winter and summer temperatures were similar among study areas (Midwest Regional Climate Center 2009; South Dakota Office of Climatology 2009; Table 1).

Deer capture and data collection.—We captured and radiocollared adult (>18 months old) and yearling (8–18 months old) female white-tailed deer during 2000–2006. We captured deer using modified Clover traps (*n* = 42—Clover 1956), helicopter net guns (*n* = 224—Brinkman et al. 2004, 2005; DePerno et al. 2002; Grovenburg et al. 2009; Jacques et al. 2009b), and immobilizing drugs delivered via a modified dart rifle (*n* = 1—Haulton et al. 2001; Dan-Inject of North America, Ft. Collins, Colorado). We equipped captured deer with very-high-frequency radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). All animal handling procedures were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval numbers 02-A043, 02-A037, 00-A038, and 04-A009) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon et al. 2007).

We located deer 2 or 3 times per week throughout the study duration using a truck-mounted null-peak antenna system (Brinkman et al. 2002). Animal locations were estimated using LOCATE II and III (Nams 2006) using a minimum of 3 azimuths for each location. To determine if winter severity influenced whether a conditional migrant migrated in any given year we calculated deer winter severity indexes (DWSIs) for each winter (1999–2007) for each study area. Winter severity was calculated using number of days with a minimum ambient temperature of ≤ -7°C (temperature index) and number of days with ≥ 35.0 cm of snow (snow index) on the ground (Brinkman et al. 2005). During November–March, severity scores were calculated with 1 point for every day that mean ambient temperature or snow depth exceeded minimum thresholds and 2 points when both conditions exceeded minimum thresholds (Minnesota Climatology Working Group 2009; South Dakota Office of Climatology 2009). We classified winter weather as mild (DWSI < 50), moderate (DWSI = 50–100), and severe (DWSI > 100—Brinkman et al. 2005).

Data analyses.—We used location estimates to determine range overlap using ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, California). For migrating animals we used known dates of migration to distinguish summer and winter seasonal ranges. For resident deer, we used mean spring and fall dates of migrations calculated from migrating animals, unique to each migrating season and study area. We classified deer as migrants if no overlap existed between seasonal ranges (Brinkman et al. 2005). We classified individuals as obligate migrators if they made a single movement to seasonal range and remained there until returning to previous seasonal range and exhibited the behavior for ≥ 3 migration periods (Brinkman et al. 2005; Sabine et al. 2002). We classified animals as conditional migrators (Nelson 1995; Nicholson et al. 1997; Sabine et al. 2002) if we documented ≥ 1 migration and they failed to migrate during any other migration period or if they made several trips to a seasonal range for <1 month (Nelson 1995). We classified deer as residents if seasonal ranges overlapped or animals failed to migrate for ≥ 3 consecutive migration periods (VerCauteren and Hygnstrom 1998). We used chi-square (χ^2) analysis to determine differences in migration classification among study sites. We conducted statistical tests using SAS version 9.2 (SAS Institute Inc. 2008) with an experiment-wide error rate of 0.05.

We followed recommendations of Bowyer and Kie (2006) and Kie et al. (2002) and used a standard shape (i.e., circle) and a set size to investigate deer ranges and habitat characteristics. Therefore, we delineated circular areas at 3 spatial scales (500-, 1,000-, and 2000-m radius) around the harmonic center (calculated from location estimates) of summer range of each deer for which we documented ≥ 3 consecutive migration periods. We chose spatial scales as representative of mean range size among study areas (Brinkman et al. 2005; DePerno et al. 2002; Grovenburg et al. 2009) rounded to the nearest 100-m radius; corresponding areas were 78.5, 314, and 1,256 ha, respectively. If we monitored a deer for >1 summer and correspondingly for >1 fall migration period, we used unique harmonic centers for each summer range and modeled variables unique to each summer and DWSIs unique to each winter for the corresponding fall migration period (i.e., multiple observations per animal). We used the 2001 National Land Cover Data (Homer et al. 2007) and measured forested cover variables at each of the 3 spatial scales using FRAGSTATS (version 3); metrics were grouped into 6 categories: patch, edge, shape, proximity, diversity, and

TABLE 2.—A priori multinomial logistic regression models constructed to determine the influence of forested cover on migration classification (i.e., resident, obligate, or conditional) of adult female white-tailed deer (*Odocoileus virginianus*) in Minnesota and South Dakota, 2000–2007.

Model[a]	Description
$FCPD_{1,000} + FCMA_{1,000} + FCSI_{1,000}$	Forest cover patch density, mean patch size, and shape index
$FCPD_{2,000} + FCMA_{2,000} + FCSI_{2,000}$	Forest cover patch density, mean patch size, and shape index
$FCPD_{500} + FCMA_{500} + FCSI_{500}$	Forest cover patch density, mean patch size, and shape index
$FCPD_{1,000} + FCMA_{1,000}$	Forest cover patch density and mean patch size
$FCPD_{500} + FCMA_{500}$	Forest cover patch density and mean patch size
$FCPD_{2,000} + FCMA_{2,000}$	Forest cover patch density and mean patch size
$FCMA_{1,000}$	Forest cover mean patch size
$FCMA_{2,000}$	Forest cover mean patch size
$FCMA_{500}$	Forest cover mean patch size
$FCPD_{1,000}$	Forest cover patch density
$FCPD_{2,000}$	Forest cover patch density
$FCPD_{500}$	Forest cover patch density

[a] FC = forested cover, PD = patch density (number of patches/100 ha), MA = mean patch area (ha), and SI = mean shape index (McGarigal et al. 2002); 500, 1,000, and 2,000 represent the buffered radius (m) around harmonic mean.

contagion (McGarigal et al. 2002). Because metrics within each FRAGSTATS category often are closely related (Hargis et al. 1988), we selected a single metric within each category (Kie et al. 2002). To test for potentially confounding relationships, we evaluated colinearity among predictor variables using Pearson's correlation coefficient ($r > |0.50|$); therefore, we present data for each of the 3 spatial scales for 3 forested cover metrics: patch density (PD: number of patches/100 ha of the habitat category), mean area (MA: mean area in ha of land-cover patches of habitat category), and landscape shape index (SI: total length of edge or perimeter involving the corresponding habitat divided by the minimum length of habitat edge or perimeter possible for a maximally aggregated habitat—McGarigal et al. 2002).

We used multinomial logistic regression to test for relationships among dependent variables (i.e., obligate migration, conditional migration, or resident) and independent variables (forested cover metrics) at each spatial scale. Deer were born on summer range and any migration to winter range was followed by a spring migration back to summer range. Deer that moved from natal summer range and never returned were classified as dispersers and not migrators (Brinkman et al. 2005; Nelson and Mech 1992) and were not included in our analyses. Therefore, we used only fall migration events and set resident deer as our reference to compare odds ratios and parameter estimates. We used cumulative migration history for each deer to classify each as permanent resident (0), conditional migrator (1), or obligate migrator (2) and modeled each fall migration event with summer habitat variables.

We used the generalized estimating equations (GEE) method to account for possible correlation among outcome variables (i.e., individuals monitored for >1 fall—Cui and Qian 2007; Molenberghs and Verbeke 2005; Pan 2001); repeated observations of an individual in a longitudinal study (i.e., outcome variable repeatedly measured on ≥2 occasions over time) were likely to be correlated because of the continuity of measurement over time (Burger et al. 2000; Cui and Qian 2007). The GEE method is an extension of the generalized linear model (Nelder and Wedderburn 1972) and enabled appropriate analysis of correlated data (Cui and Qian 2007). The GEE method with repeated measures returns intercept and parameter estimates to $\rho - 1$ (where ρ is the number of response variables) cumulative logits in the form of $\log(\rho_1/1 - \rho_1)$, $\log[(\rho_1 + \rho_2)/1 - (\rho_1 + \rho_2)]$, and so forth (Molenberghs and Verbeke 2005; SAS Institute Inc. 2008).

We generated 12 a priori models (Table 2) and used quasi-likelihood under the independence model criterion (QIC) for GEE to select models that best described the data (Cui and Qian 2007; Hardin and Hilbe 2003; Pan 2001; SAS Institute Inc. 2008). The GEE method is based on quasi-likelihood theory (Wedderburn 1974) and not maximized-likelihood theory for independent observations (generalized linear model method—McCullagh and Nelder 1989). Consequently, model selection statistics such as Akaike's information criterion (Burnham and Anderson 2002) developed under the maximum-likelihood theory cannot be applied directly to the GEE method (Cui and Qian 2007; SAS Institute Inc. 2008). In a comparison of models with QIC, the model with the smaller QIC statistic is preferred and is appropriate for selecting regression models; we considered models differing by ≤2 ΔQIC from the selected model as potential alternatives (Pan 2001; SAS Institute Inc. 2008). We used Shapiro–Wilk W to test important habitat variables for normality and box plots to test for homoscedasticity. We used analysis of variance to determine differences in important habitat variables among the classifications and Tukey's test for pairwise comparisons.

We used logistic regression to assess the influence of winter severity on whether conditional migrants migrate in any given fall. For conditional migrations, we modeled each fall deer-migration season to its corresponding DWSI, temperature index, and snow index using logistic regression by assigning a value of 0 if an animal failed to migrate and 1 if the animal migrated. We used the Hosmer and Lemeshow goodness-of-fit (χ^2) test to determine model fit ($P > 0.05$ indicated appropriate model fit—Hosmer and Lemeshow 2000).

TABLE 3.—Percentage migratory classification (see ''Materials and Methods''), deer winter severity index (DWSI), and number of adult female white-tailed deer (*Odocoileus virginianus*) monitored for ≥3 migratory seasons at 7 study sites in Minnesota and South Dakota, 2000–2007.

Site[a]	Obligate (%)	Conditional (%)	Resident (%)	DWSI[b]	No. deer
BEFM	52.9	14.7	32.4	36–63	34
B	43.8	18.8	37.5	59–69	16
G	66.7	0.0	33.3	61–67	9
FO	9.1	9.1	81.8	33–94	22
RD	41.7	58.3	0.0	49–95	12
RN	32.4	50.0	17.7	43–150	34
LP	69.6	26.1	4.4	57–167	23

[a] Study sites: BEFM = Brown, Edmunds, Faulk, and McPherson counties; B = Brookings County; G = Grant County; FO = Fillmore and Olmsted counties; RD = Redwood County; RN = Renville County; and LP = Lincoln and Pipestone counties.
[b] DWSI calculated according to Brinkman et al. (2005) during November–March (Minnesota Climatology Working Group 2009; South Dakota Office of Climatology 2009).

RESULTS

We captured 267 female white-tailed deer and monitored 149 through ≥3 seasonal migration periods from 2000 to 2007. We captured deer at multiple locations throughout each study area, including winter and summer range areas, from January to April over varying winter severities ranging from mild to severe; percent captured deer was approximately equal between summer and winter ranges. We censored 118 deer that we failed to monitor for ≥3 migration seasons because of mortality, dispersal, or lost contact. We documented 585 deer-migration seasons and mean ($\pm$ *SD*) number of seasonal migration periods for animals monitored through ≥3 seasonal migration periods was 4.3 $\pm$ 1.6 (*n* = 149, range 3.0–9.0). We classified 63 (42%) animals as obligate migrators, 30 (20%) as conditional migrators, and 56 (38%) as permanent residents. Across study sites, percentage of obligate and conditional migrators ranged from 9% to 70% and 0% to 58%, respectively, and percentage of residents ranged from 0% to 82% (Table 3). Migration classification differed (χ^2_{12} = 39.31, *P* < 0.001) among study sites. All deer classified as obligate migrators with ≥3 migrations (range 3–9 migration seasons) maintained their obligate status for the duration of the study. We observed no change in obligate classification due to duration of monitoring despite low values of DWSI or monitoring through consecutive (≥2) mild winters. Similarly, we observed no change in resident or conditional classification due to monitoring through consecutive (≥2) moderate to severe winters. Deer classified as conditional migrants did not migrate during 118 deer-migration seasons. Mean number of documented migrations for obligate and conditional migrators was 4.6 $\pm$ 1.8 (*n* = 63, range 3–9) and 1.5 $\pm$ 0.3 (*n* = 30, range 1–2), respectively, and 45.5% of obligate migrators were monitored ≥3 years (Fig. 2). Because seasonal ranges always were separated by ≥2 radii, the risk of falsely categorizing a migrating deer as a resident was minor.

We selected the model with the lowest QIC value (FCPD$_{1,000}$ + FCMA$_{1,000}$; QIC weight = 0.81); remaining
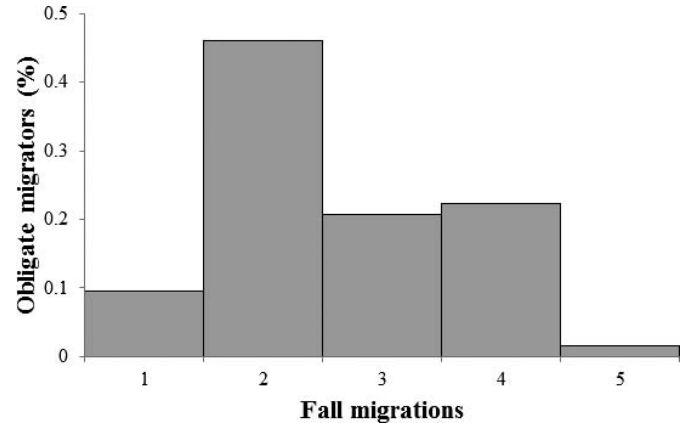
FIG. 2.—Percent of obligate migrating adult female white-tailed deer (*Odocoileus virginianus*) that were monitored in Minnesota and South Dakota, 2000–2007, for the number of fall migration periods indicated.

models were ≥2.92 ΔQIC units from the top model (Table 4). Parameter estimates indicated significant variable effects (Table 5) and the type 3 test indicated that forest cover patch density (FCPD; χ^2_1 = 16.47, *P* < 0.001) and forest cover mean area (FCMA; χ^2_1 = 14.79, *P* < 0.001) were significant. Multinomial logistic odds ratios using the logits acquired from the GEE model indicated the odds of being a resident (versus conditional and obligate migrator) increased by 1.4 (95% confidence interval [95% *CI*] = 1.14–1.58) per 1-unit increase in forest cover PD and by 1.3 (95% *CI* = 1.19–1.51) per 1-unit increase in forest cover MA. Multinomial logistic odds ratios indicated the odds of being an obligate migrator (versus resident and conditional migrator) increased by 0.7 (95% *CI* = 0.63–0.87) per 1-unit decrease in forest cover PD and by 0.8 (95% *CI* = 0.66–0.84) per 1-unit decrease in forest cover MA.

We assessed mean values of habitat variables in FCPD$_{1,000}$ + FCMA$_{1,000}$ among migration categories (i.e., resident, obligate, and conditional). Mean PD ($F_{2,347}$ = 46.20, *P* < 0.001) and MA ($F_{2,347}$ = 34.29, *P* < 0.001) differed among migration categories; MA decreased with increasing PD (Fig. 3). Relative to forest cover in resident habitat areas, obligate and conditional migrators had smaller (*P* < 0.001) mean PD and MA (ha) of forested habitat within buffered areas (Fig. 4). With respect to comparing obligate to conditional migrators, obligate habitat areas had smaller (*P* < 0.001) mean PD and MA of forested habitat than conditional migrators (Fig. 4).

Average DWSI values ranged from 33 to 167 (Table 2). Whether a conditional migrator migrated in any given fall was related to DWSI (β_0 = −5.93, *SE* = 1.64; β_1 = 0.09, *SE* = 0.03), and goodness-of-fit test results (χ^2_8 = 15.22, *P* = 0.072) indicated appropriate model fit. Odds ratio point estimates indicated that DWSI (1.094, 95% *CI* = 1.039–1.152) influenced conditional migration during deer-migration seasons (Fig. 5). However, goodness-of-fit tests for logistic models for snow (χ^2_4 = 10.39, *P* = 0.034) and temperature (χ^2_7 = 20.60, *P* = 0.004) indicated poor model fit. Consequently, we did not consider that snow or temperature

TABLE 4.—Top-ranked a priori multinomial logistic regression models using the generalized estimating equations (GEE) method for migration classification (i.e., resident, conditional, or obligate) using quasi-likelihood under the independence model criterion (QIC) for GEE of adult female white-tailed deer (*Odocoileus virginianus*) in Minnesota and South Dakota, 2000–2007.

Model[a]	QIC[b]	ΔQIC[c]	w_i[d]
$FCPD_{1,000} + FCMA_{1,000}$	590.34	0.00	0.81
$FCPD_{1,000} + FCMA_{1,000} + FCSI_{1,000}$	593.26	2.92	0.19
$FCPD_{500} + FCMA_{500}$	604.70	14.37	0.00
$FCPD_{2,000} + FCMA_{2,000} + FCSI_{2,000}$	606.96	16.63	0.00

[a] FC = forested cover, PD = patch density (number of patches/100 ha), MA = mean patch area (ha), and SI = mean shape index (McGarigal et al. 2002); 500, 1,000, and 2,000 represent buffered radius (m) around harmonic mean.

[b] Quasi-likelihood under the independence model criterion for GEE (Cui and Qian 2007; Hardin and Hilbe 2003; Pan 2001; SAS Institute Inc. 2008).

[c] Difference in QIC relative to minimum QIC.

[d] QIC model weight.

covariates individually influenced migration of conditional migrants.

DISCUSSION

Because we concentrated capture activities on both winter and summer range areas, we assumed wider distribution of capture effort (e.g., on and off winter areas) might have led to improved estimates of migration classification (i.e., resident, conditional, and obligate—Fieberg et al. 2008). Our hypothesis that greater patch density, larger mean patch size, and increased irregular-shaped forested patches would result in greater proportion of resident deer was supported only partially by our results. Although greater patch density and larger mean patch size were associated with an increase in percentage of residents, shape index as a measure of amount and irregularity of edge did not influence classification. Because forest patch density and mean patch size in summer range exceeded 2.7 patches/100 ha and 1.2 ha, respectively, deer were more likely to be residents than migrators. Although not specifically tested in our study, this behavioral response could relate to less vulnerability to predation with increased

TABLE 5.—Multinomial logit parameter estimates and robust standard error using the generalized estimating equations (GEE) method for the top-fitted model ($FCPD_{1,000} + FCMA_{1,000}$) for adult female white-tailed deer (*Odocoileus virginianus*) in South Dakota and Minnesota, 2000–2007. The GEE method with repeated measures returned intercept and parameter estimates to 2 cumulative logits ($\log(\rho_1/1 - \rho_1)$ and $\log[(\rho_1 + \rho_2)/1 - (\rho_1 + \rho_2)]$—Molenberghs and Verbeke 2005; SAS Institute Inc. 2008).

| Parameter[a]	Estimate	*SE*
Intercept 1	−2.00*	0.33
Intercept 2	−0.73*	0.24
FCPD	0.30*	0.08
FCMA	0.29*	0.06

[a] FC = forested cover, PD = patch density (number of patches/100 ha), MA = mean patch area (ha).

* $P < 0.001$.
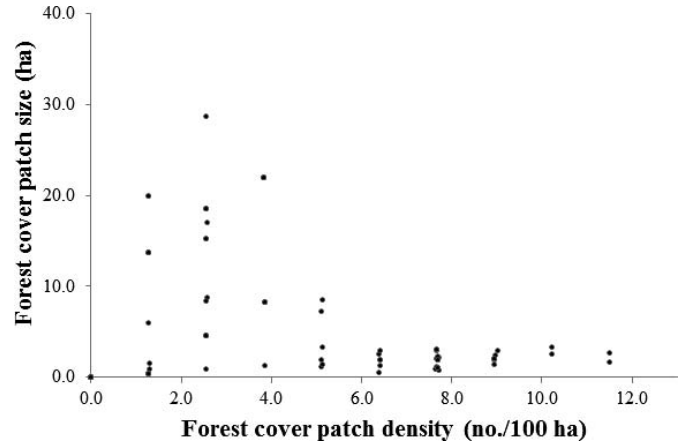
FIG. 3.—Mean forest cover patch density (number of patches/100 ha) as a function of mean forest cover patch size (ha) for a 1,000-m-radius buffer around harmonic center of range area for adult female white-tailed deer (*Odocoileus virginianus*) in Minnesota and South Dakota, 2000–2007.

patch size and availability of escape cover (Barbour and Litvaitis 1993; Brown and Litvaitis 1995; Kunkel and Pletscher 2000; Rohm et al. 2007; Stuart-Smith et al. 1997). For instance, large forest patches are more difficult for predators to search completely and might be searched less often (Andren and Angelstam 1988; Brown and Litvaitis 1995;
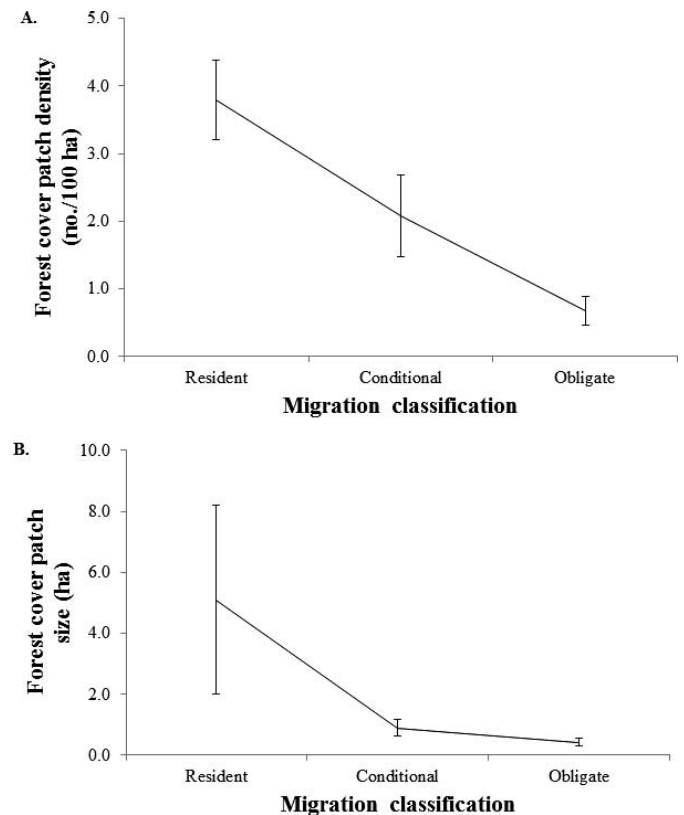
FIG. 4.—Mean forest cover A) patch density and B) patch size, with 95% confidence intervals, for resident, conditional migrating, and obligate migrating adult female white-tailed deer (*Odocoileus virginianus*) in Minnesota and South Dakota, 2000–2007.
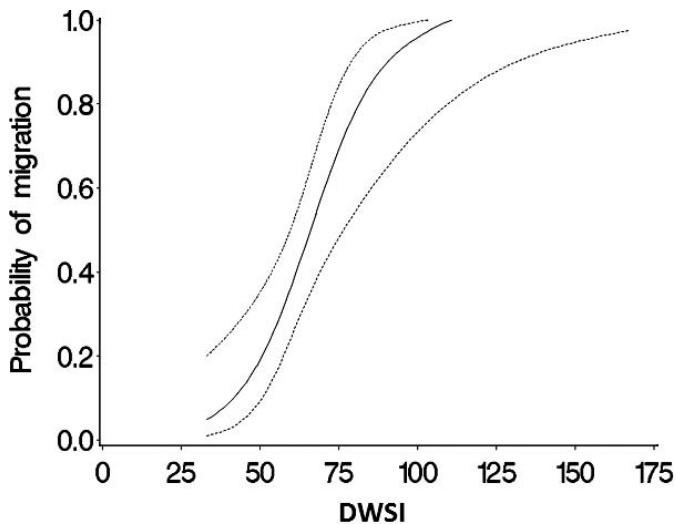
Fig. 5.—Logistic regression with 95% confidence limits indicating the probability that adult female white-tailed deer (*Odocoileus virginianus*) classified as conditional migrators (i.e., those monitored for ≥ 3 migration seasons that migrated ≥ 1 migration seasons and were also nonmigratory ≥ 1 migration seasons) migrated in any given year as a function of deer winter severity index (DWSI) experienced by each deer monitored during each fall migration season (ln y = $-5.93 + 0.09$ [DWSI]), in Minnesota and South Dakota, 2000–2007.

Phillips et al. 2003). Additionally, coyotes (*Canis latrans*), the main predators on ungulates in our study area (Brinkman et al. 2004; Grovenburg et al. 2011; Turner et al., in press), are less efficient predators in forested landscapes than in more open areas (Gese et al. 1996; Richer et al. 2002; Rohm et al. 2007).

Multiple large patches of forested cover likely provided deer with refugia (Rohm et al. 2007), resulting in increased adult survival and potentially increased reproductive fitness for adult females through increased survival of neonates. The landscape pattern of large patches of forested cover interspersed with patches of forage habitat (i.e., cultivated land) might allow females to maintain smaller home ranges, thereby allowing increased time for maternal care (Rohm et al. 2007). During our study home-range size was greater for migrating individuals than for residents, suggesting that increased forest patch density and patch size could have provided resident deer with a hypothesized ''psychological security'' (Naugle et al. 1997), allowing animals to be active while remaining in close proximity to escape cover.

Migration was more likely in habitats with fewer patches of forest and smaller forest patch size. When forest patch density and mean patch size in summer range areas were ≤ 0.9 patches/100 ha and 0.6 ha, respectively, deer were more likely to exhibit obligate migration. Similarly, when forest patch density and mean patch size in summer range areas ranged between 0.9 and 2.7 patches/100 ha and 0.6 and 1.2 ha, respectively, deer were more likely to be conditional migrants. In grassland regions, permanent escape cover (i.e., forested cover) often is limited and fragmented (Dusek et al. 1989; Smith et al. 2002), and costs of migration can differ regionally

with land cover and distribution, composition, and relative abundance of predator populations.

Despite pronounced temporal variation in winter severity throughout our study, we documented no variation among deer classified as obligate migrators (monitored 3–9 migration seasons), as was documented in northern Minnesota (Fieberg et al. 2008). However, we did document that conditional migrators were more likely to initiate migration as severity of winter weather increased, particularly in response to ambient temperatures $\leq -7°C$ (Nelson 1995; Tierson et al. 1985), which likely is the primary cue triggering migration events across the Northern Great Plains (Grovenburg et al. 2009). Synergistic effects of increased snow depth and decreased temperatures were reported to initiate migration to winter range (Brinkman et al. 2004; Drolet 1976; Nelson 1995; Ozoga and Gysel 1972; Verme 1968). Our results support other studies conducted on deer along the northern edge of their geographic distribution.

The Northern Great Plains historically was inhabited by mule deer (Severson 1981) and white-tailed deer (Petersen 1984). White-tailed deer, although occurring throughout the region, were associated with draws, swales, and lowlands characterized by riparian vegetation (Dusek et al. 1989; Petersen 1984). Woodlands continue to represent a limited habitat in the region due to human-induced modification (e.g., planting of shelterbelts) to minimize soil loss in adjacent agricultural land. Deer in the Northern Great Plains disperse long distances in search of suitable habitat (Brinkman et al. 2005; Kernohan et al. 2002; Long et al. 2005), likely due to the patchwork distribution of these small woodlands and shelterbelts (Smith et al. 2002). Similarly, long migration distances (Brinkman et al. 2005; Grovenburg et al. 2009) mirror dispersal distances in this region. Our results indicated that patch size and density of forested cover and winter severity influenced deer migration strategies. Because of the importance of forest fragments to migration, anthropogenic disturbance of these habitat patches likely affects long-term movements and stability of residents within the Northern Great Plains.

Ability to predict population-specific migration strategies can have important implications for conservation, population dynamics, and species management, especially in an increasingly fragmented environment (Forman 1995). For instance, seasonal movements such as migration and dispersal have been suggested as a means of spreading chronic wasting disease to new foci of infection (Belay et al. 2004). Deer movement between seasonal ranges would facilitate exposure of both conspecifics and susceptible sympatric species to infected prions shed by symptomatic and asymptomatic animals (Tamgüney et al. 2009). Additionally, increased understanding of migration probabilities and distances can improve understanding of factors contributing to variation in spatial distribution of deer, recolonization rates, and population turnover in fragmented habitats. Ultimately, greater understanding of migration strategies can improve predictive capabilities of population models for use in better-informed

decision-making processes and thus, conservation and management of deer populations throughout the Northern Great Plains and elsewhere. However, additional work addressing fitness benefits and costs of migration in environments with minimal predation is warranted.

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