Management and Conservation Article

Associating Seasonal Range Characteristics With Survival of Female White-Tailed Deer

ROBERT W. KLAVER,[1] *United States Geological Survey Center for Earth Resources Observation and Science, Sioux Falls, SD 57198, USA*

JONATHAN A. JENKS, *Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD 57007-1696, USA*

CHRISTOPHER S. DEPERNO, *Fisheries and Wildlife Sciences Program, Department of Forestry and Environmental Research, North Carolina State University, Raleigh, NC 27695-7646, USA*

STEVEN L. GRIFFIN, *South Dakota Department of Game, Fish, and Parks, Rapid City, SD 57702, USA*

ABSTRACT Delineating populations is critical for understanding population dynamics and managing habitats. Our objective was to delineate subpopulations of migratory female white-tailed deer (*Odocoileus virginianus*) in the central Black Hills, South Dakota and Wyoming, USA, on summer and winter ranges. We used fuzzy classification to assign radiocollared deer to subpopulations based on spatial location, characterized subpopulations by trapping sites, and explored relationships among survival of subpopulations and habitat variables. In winter, Kaplan–Meier estimates for subpopulations indicated 2 groups: high ($S = 0.991 \pm 0.005$ [$\bar{x} \pm$ SE]) and low ($S = 0.968 \pm 0.007$) weekly survivorship. Survivorship increased with basal area per hectare of trees, average diameter at breast height of trees, percent cover of slash, and total point-center quarter distance of trees. Cover of grass and forbs were less for the high survivorship than the lower survivorship group. In summer, deer were spaced apart with mixed associations among subpopulations. Habitat manipulations that promote or maintain large trees (i.e., basal area = 14.8 m^2/ha and average dbh of trees = 8.3 cm) would seem to improve adult survival of deer in winter. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):343–353; 2008)

DOI: 10.2192/2005-581

KEY WORDS Black Hills, fuzzy classification, habitat use, *Odocoileus virginianus,* scale, South Dakota, survivorship, white-tailed deer.

Habitat selection occurs at multiple scales influenced by conspecifics, predators, and the environment, which affects individual survival and reproductive rates and, thus, fitness (Svärdson 1949, Hilden 1965, Levins 1968). Habitat studies generally have relied on presumed benefits of relative use and activities in various habitats to assess fitness benefits. However, without corresponding demographic data, conclusions about habitat quality may be spurious (Van Horne 1983, Pulliam 1988, Garshelis 2000, Millspaugh and Marzluff 2001). Kirsch (1996) suggested that proximate habitat features might not be indicative of habitat suitability or reveal potential selective pressures influencing habitat selection. Kirsch (1996) recommended that factors influencing fitness be directly related to habitat features. Moreover, Garshelis (2000), in criticizing habitat evaluation studies, recommended comparison of frequency of use of different habitats to habitat composition of home ranges in relation to reproduction and survival.

Delineating populations is critical for understanding population dynamics and managing habitat. However, populations are generally not sharply defined except in highly fragmented landscapes (Bethke et al. 1996, Schaefer et al. 2001). Spatiotemporal connectivity is increasingly used to delineate populations. Social organization and population substructure may be determined by resource availability resulting in individual life-history parameters varying among population segments (Clutton-Brock and Harvey 1978, Sutherland 1996). Small-scale spatial variation in life-history parameters may occur within populations without obvious substructures (Coulson et al. 1999, Focardi et al. 2002, Pettorelli et al. 2003*a*, Zannèse et al. 2006). Recently, several studies used traditional classification techniques to describe bear (*Ursus* spp.) subpopulations (Bethke et al. 1996, Taylor et al. 2001, McLoughlin et al. 2002, Mauritzen et al. 2002). Moreover, Coulson et al. (1997, 1999) documented subpopulations of red deer (*Cervus elaphus*) and soay sheep (*Ovis aries*) that exhibited differences in survival, recruitment, and dispersal rates. Coulson et al. (1999) asserted the lack of information on small-scale spatial population dynamics was due to lack of techniques for subdividing populations.

Schaefer et al. (2001) and Schaefer and Wilson (2002) used fuzzy clustering to delineate subpopulations of caribou (*Rangifer tarandus*) in the Red Wine Mountains, Quebec-Labrador, Canada, that displayed variation in population rates. Whereas traditional cluster analysis places items into distinct classes, fuzzy clustering categorizes items displaying continuous variation into classes without distinct boundaries (Schaefer and Wilson 2002). Fuzzy membership coefficients vary between zero and one; thus, classes convey a degree of membership. Optimum values for degree of fuzziness and number of classes are required to balance structure and continuity of clustering (McBratney and Moore 1985, Odeh et al. 1992). Output of a fuzzy classification is not uncertain but strictly deterministic. Thus, fuzzy classification provides multiple options for display and analysis of spatial data (Marsili-Libelli 1989, Brown 1998).

Our objective was to delineate subpopulations of migratory female white-tailed deer (*Odocoileus virginianus*) in the central Black Hills, South Dakota and Wyoming, USA, on summer and winter ranges. We assumed no spatial clustering of deer among trapping areas due to winter

[1] *E-mail: bklaver@usgs.gov*

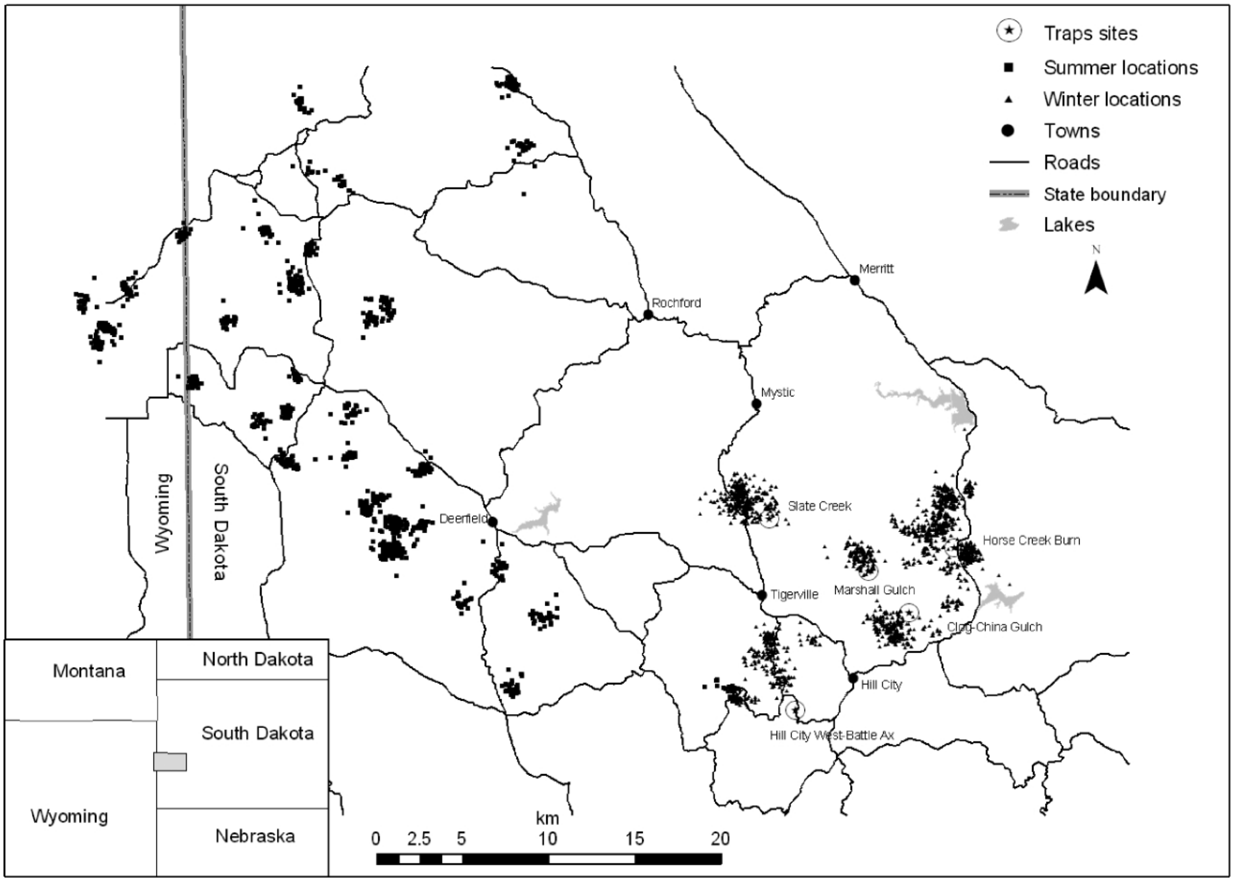


Figure 1. Location of the winter and summer ranges of white-tailed deer in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. Winter and summer locations of female white-tailed deer are indicated by triangles or squares, respectively. Locations of the 5 trap sites (Slate Creek, Marshall Gulch, Horse Creek Burn, Clog–China Gulch, and Hill City West–Battle Ax) are shown. Inset map shows the Black Hills National Forest and the study area shaded in gray.

conditions, snow depth, deer movements, and home range size. We predicted that deer in the same subpopulation would move together between winter and summer ranges (Nelson and Mech 1987). Additionally, we determined the relationship between survivorship and habitat characteristics within these subpopulations. We predicted that in winter deer with higher survivorship would select locations with higher cover values than would deer with poorer survivorship. In summer, we predicted that deer with higher survivorship would select areas with better forage than would deer with lower survivorship.

STUDY AREA

The Central Black Hills is located in western South Dakota and northeastern Wyoming (43°52′N to 44°15′N–104°7′W to 103°22′W) within Pennington and Lawrence counties in South Dakota and Crook and Weston counties in Wyoming. Summer and winter ranges of migratory white-tailed deer are encompassed within the region and deer migrated an average of 32 km (5–56 km) between seasonal ranges (Griffin et al. 1999). Elevations varied between 915 m and 2,207 m above mean sea level with winter range located at elevations <1,829 m (Sieg and Severson 1996). Climate was continental; mean annual temperature varied from 5° C to 9° C with extremes of −40° C to 44° C. Strong temperature inversions were common during winter, with higher elevations experiencing warmer temperatures than lower elevations (Thilenius 1972). Vegetation of the region was described in detail by DePerno et al. (2002). In addition, a burn pine class was identified by the South Dakota GAP Analysis Program vegetation mapping project as a unique vegetation type within the 8,900-ha McVey fire perimeter that occurred in 1939 (Griffin et al. 1999, Smith et al. 2002). Within this region, we selected 5 winter areas for deer trapping, Slate Creek, Marshall Gulch, Horse Creek, Battle-Ax, and Clog–China Gulch (Fig. 1) that were naturally separated by rock terraces and diverging draws (Osborn 1994, Griffin et al. 1995, Hippensteel 2000).

The Black Hills National Forest administered approximately 80% of the Black Hills. Predominant land uses were timber production, cattle grazing, second home development, and big game winter range. Other ungulates inhabiting the area were mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), and cattle (*Bos taurus*). Potential predators were mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and domestic dogs.

METHODS

Deer Locations and Seasonal Ranges

A detailed description of methods used to capture and radiocollar deer in the central Black Hills was provided by DePerno (1998) and Griffin et al. (1995). We captured deer February to March 1993–1996 in Clover traps baited with fresh alfalfa (*Medicago sativa*) hay at 5 sites on winter range (Fig. 1; Clover 1956, Griffin et al. 1995). Each trap site had 5–10 clover traps in the general area of 1.6 km from the central location; we moved traps to new sites weekly, from February to March. We fitted deer ($n = 73$) with radiocollars, then ear-tagged and released them. We excluded from analyses data on a radiocollared female that demonstrated an abnormal migration pattern (DePerno et al. 1997). We ground-tracked deer 1–3 times per week between March 1993 and June 1996. We walked to each deer location, verified its location, and collected habitat measurements. If the animal was disturbed, we performed a general habitat description (e.g., stand type); however, if the animal was undisturbed, specific habitat measurements (e.g., basal area, dbh of trees) were collected. Radio relocations were within 100 m of actual deer locations, mainly due to the accuracy of determining Universal Transverse Mercator (UTM) locations on 1:24,000 scale maps. We collected relocations at different time-periods throughout the day to maximize observations of diurnal activities, while avoiding violating the assumption of independence (White and Garrott 1990). Our sampling design provided an unbiased estimate of 24-hour habitat use (Hayes and Krausman 1993, Kernohan et al. 1996). We categorized relocations of white-tailed deer by activity as either bedding or feeding.

We determined seasonal ranges of individual deer from visual inspection of mapped locations plotted sequentially by date. We stratified locations of individual deer into summer, transitional, winter, and migration, by inspecting the spatial and temporal distribution of locations. We considered clustered locations a seasonal range (D'Eon and Serrouya 2005). Summer locations were generally May through October, whereas winter locations were November through April (Fig. 2). We considered locations not part of clusters at either the beginning or end of a season as migratory. We defined site fidelity at the drainage level rather than a shift within a drainage (White and Garrott 1990, Powell 2000). After testing that combining years would not mask differences in site fidelity, we pooled relocations of deer across years (Schooley 1994, Klaver 2001).

Fuzzy Clustering

Contrary to previous studies that used median values, we used harmonic means of UTM eastings and northings of deer locations to determine central tendency of locations because harmonic means are constrained to fall within seasonal ranges, are insensitive to extreme locations, must be located in regions where density of locations is high relative to density in remaining areas, and are insensitive to movements within populations (Neft 1966, Bethke et al. 1996, Schaefer et al. 2001, Taylor et al. 2001). To determine sample size for calculating harmonic centers, we drew samples of 10, 15, 20, and 25 locations from locations of animals with $\geq$30 locations. We report error as the distance from harmonic centers from these samples to the harmonic center using all locations.

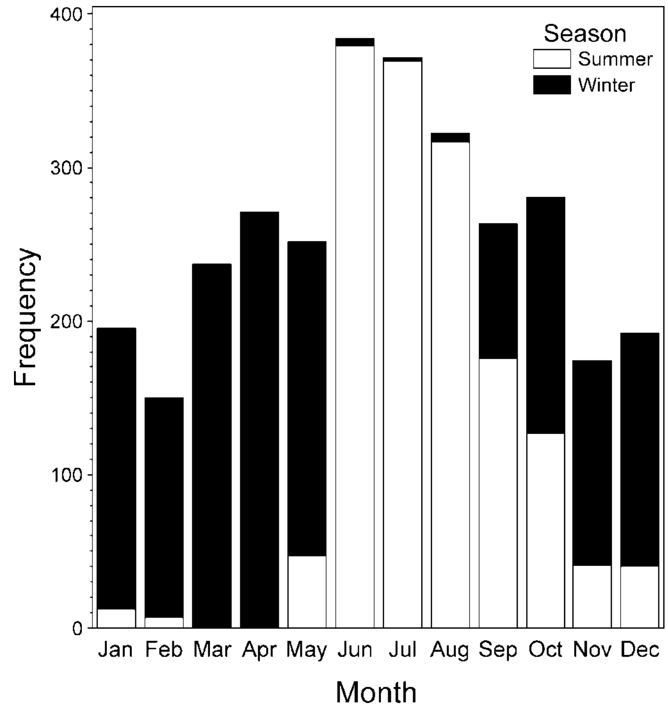


Figure 2. Monthly distribution of number of summer and winter locations of female white-tailed deer in central Black Hills, South Dakota and Wyoming, USA, 1993–1996.

We grouped harmonic centers of individual deer locations into subpopulations using the fuzzy *k*-means classification program FuzME version 3 (Minasny and McBratney 2002). We used diagonal distance transformation to standardize measurements used in the classification to equal variance (McBratney and Moore 1985, Odeh et al. 1992). This diagonal distance transformation prevented UTM northings from dominating UTM eastings. When degree of fuzziness (ϕ) equals 1, classification is identical to a hard classification such as the isoclass algorithm; as ϕ becomes larger, assignment to classes becomes fuzzier (Equihua 1990). We used the method of Odeh et al. (1992) of plotting the partial derivative of group sum of squares ($\mathbf{J}_m$) multiplied by the square root of number of classes (c; i.e., $[-\delta \mathbf{J}_m/\delta\phi]c^{1/2}$, or slope) against degree of fuzziness (ϕ) to determine local maxima of ϕ. We plotted minimum values of fuzziness performance index, F', and the normalized classification entropy, or modified partition entropy, H', against number of classes; we used local minima to determine number of classes (McBratney and Moore 1985). Although somewhat subjective, these plots may be used to reveal optimum values for degree of fuzziness and number of classes that balance structure and continuity of clustering (McBratney and Moore 1985, Odeh et al. 1992).

Microhabitat Measurements

Variables we considered in habitat analyses were microhabitat characteristics of forest stands (DePerno 1998; DePerno et al. 2000, 2001, 2002). We collected these variables at point locations obtained via ground-tracking radiocollared white-tailed deer. We measured basal area (m^2/ha; BA_HA) using a 10-factor angle gauge (Hovind and Reick 1970). We measured diameter at breast height of trees (cm; DBH) at 1.37 m above ground to the nearest cm with a diameter tape. Average diameter at breast height (cm; AVEDBH) was the average of each tree in the basal area count. Shrub and tree saplings were >1 m in height and <5 cm diameter at breast height. Number of shrub or tree saplings (stems/ha; TSSTOT) was the average counted in 2 perpendicular, 1 $m^2 \times$ 20-m belt transects oriented north–south and east–west intersecting at plot center. We measured percent canopy cover of conifers (CONCOV) and deciduous trees (DECIDCOV) with a spherical densiometer (Lemmon 1956). We determined percent ground cover of grass (GRASS), forbs (FORBS), sticks >2.54 cm diameter (SLASH), and shrubs <1 m in height (SHRUBS) from 15 1-m^2 plots systematically spaced within the 400-m^2 plots (Daubenmire 1959). Point-centered quarter distance (TPCQDIST) was the average distance (m) from the plot center to the nearest basal-area tree in each of the 4 quadrants (Cottam and Curtis 1956). We measured visual obstruction using a 1-m^2 cloth divided into 100 10-cm squares (Bowyer 1986). We took readings 10 m from plot center and 1 m above ground in each of the 4 cardinal directions. Low visual obstruction (TVOL), an estimate of cover available to bedded deer, was the total of the bottom 50 squares (0.0–0.5 m); high visual obstruction (TVOH), an estimate of cover available to standing deer, was the total of the top 50 squares (0.5–1.0 m; Bowyer 1986). Additionally, we estimated the average of the 4 distances (m) at which 90% of the cloth was concealed (TVODIS).

Statistical Analysis

We calculated Kaplan–Meier survivor estimates using the known-fate routine in program MARK (Pollock et al. 1989, White and Burnham 1999). We developed encounter histories for the 42 months between January 1993 and June 1996. We first assigned deer to a subpopulation based on the maximum class from the fuzzy classification. We visually assigned deer with fewer locations to a subpopulation based on their locations and the locations of the subpopulation. We calculated survivorship of the subpopulations for each seasonal range using 2 methods. First, we determined the effect of winter subpopulation on individual survivorship. Secondly, we calculated individual survivorship using fuzzy membership as a covariate. We ranked competing models using Akaike's Information Criterion corrected for small sample size and Akaike importance value (Burnham and Anderson 2002). We used a 2-factor multivariate analysis of variance (MANOVA) based on rank transformation of the variables to compare habitat characteristics by survivorship group and activity type (feeding or bedded) and their interaction (PROC GLM in SAS; SAS Institute, Cary, NC; Conover and Iman 1981). We evaluated significance with Type III sum of squares. If the interaction term was not significant we reported the survivorship group main effect on microsite variables. We set $\alpha = 0.10$ (Morrison et al. 1998).

Table 1. Mean, median, and range in error as measured by distance between harmonic centers subsampled from female white-tailed deer with ≥30 locations and harmonic centers calculated using all locations in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. We drew subsamples of 10, 15, 20, and 30 locations to determine minimum sample size for calculating harmonic centers for summer and winter analyses.

		Error		
Season	*n*	$\bar{x}$ (m)	Median (m)	Range (m)
Summer	10	170.7	118.2	1,745.6–5.8
	15	146.1	100.2	1,126.1–18.8
	20	126.3	79.2	821.4–10.7
	25	97.1	46.7	629.3–7.6
	30	79.0	37.9	498.0–0.0
Winter	10	237.3	179.6	1,083.6–20.7
	15	196.5	162.6	633.4–30.9
	20	158.3	120.9	550.4–31.0
	25	126.5	107.3	383.0–18.6
	30	112.2	75.4	393.5–0.0

RESULTS

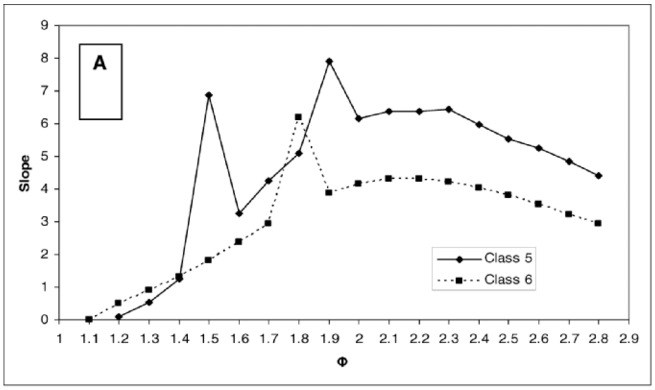
Winter

We calculated the harmonic mean of the distribution of 916 locations for each deer with >14 locations ($n = 37$); maximum error using 15 observations was <633 m (196 ± 149 m [$\bar{x} \pm$ SD]; Table 1). Fuzzy classification identified 6 classes using degree of fuzziness (ϕ) = 2.1 (Figs. 3, 4; Table 2). The plot of $(-\delta \mathbf{J}_m/\delta\phi)c^{1/2}$ against ϕ (Fig. 3A) had its least maximum with 6 classes and $\phi = 2.1$. Moreover, plots of fuzziness performance index (F') and normalized classification entropy (H') against the number of classes both revealed local minima at 6 classes (Fig. 3B).

There was correspondence between the 5 trap sites on winter ranges and 6 subpopulations identified using the fuzzy classifier (Fig. 4). The additional subpopulation (i.e., D) separated deer using burned-pine cover types from those using other cover types on the Horse Creek winter range. The classifier did not identify deer 1330b with those using the burned-pine cover (i.e., subpopulation D) but membership was highly mixed.

Kaplan–Meier survival analysis using subpopulation as a covariate identified 2 groups (Table 3). Subpopulations C and D (Fig. 4) had higher weekly survivorship (0.991 ± 0.005 [$\bar{x} \pm$ SE]) than the other subpopulations (0.968 ± 0.007). Subpopulation D inhabited the burned-pine cover type. Survival analysis using fuzzy-group membership to winter subpopulation C indicated that subpopulation membership was an important variable explaining individual survival (Table 4). The importance value of the Akaike weights for fuzzy membership was 0.6.

The MANOVA survivorship group × activity interaction



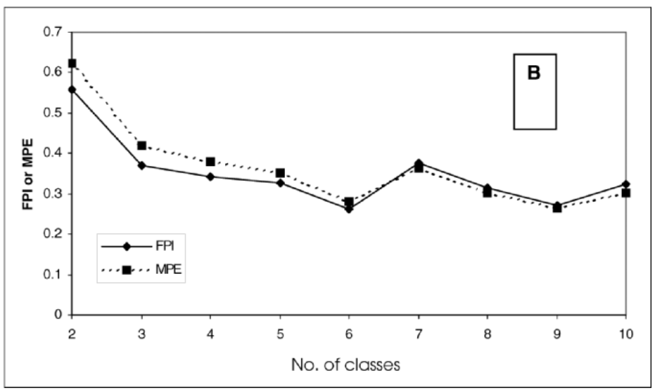


Figure 3. Relationship between number of classes and the degree of fuzziness, ϕ, for classification of female white-tailed deer on winter range in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. A) Relationship between slope, $(-\delta \mathbf{J}_m/\delta\phi)c^{1/2}$, and ϕ, for both 5 and 6 classes. We chose a value of $\phi = 2.1$ because both 5 and 6 classes were a maximum at this value. B) Relationship between fuzziness performance index, FPI, and modified partition entropy (MPE), H', with $\phi = 2.1$. Both FPI and H' indicate local minimum at 6 classes.

Table 2. Seasonal characteristics of white-tailed deer subpopulations in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996, indicating the number of deer in each subpopulation with the number of additional deer assigned to the population for survival analysis and the number of microvegetation plots on winter range.

Winter	*N*	No. plots	Summer	*N*
A	4[a]	25	A	9[b]
B	5	28	B	8
C	7	44	C	1
D	6	67	D	4
E	8	41	E	6
F	7	46	F	5
			G	2

[a] Additional deer assigned for winter A: 3; B: 9; C: 2; D: 3; E: 11; F 9.
[b] Additional deer assigned for summer A: 8; B: 5; C: 1; D: 2; E: 4; F: 1; G: 1.

was not significant (Wilk's $\lambda = 0.921$, $F_{14,234} = 1.44$, $P = 0.134$). Results of MANOVA for the survivorship main effect differences were significant (Wilk's $\lambda = 0.858$, $F_{14,234} = 2.76$, $P = 0.001$) for the variables BA_HA ($P = 0.084$), AVEDBH ($P = 0.001$), GRASS ($P = 0.001$), FORBS ($P = 0.066$), SLASH ($P \leq 0.001$), and TPCQDIST ($P = 0.004$). Variables BA_HA , AVEDBH , SLASH, and TPCQDIST were 11%, 19%, 31%, and 21% greater, respectively, for the high compared to the low survivorship group; GRASS and FORBS were 7% and 22% lower, respectively, for the high compared to the low survivorship group (Table 5).

Summer

We calculated the harmonic mean of the distribution of 1,756 locations for each deer with >19 locations ($n = 35$); maximum error using 20 observations was <821 m (126 ± 147 m [$\bar{x}$ ± SD]; Table 1). Fuzzy classification identified 7 classes using $\phi = 1.9$ (Figs. 5, 6; Table 2). The plot of $(-\delta \mathbf{J}_m/\delta\phi)c^{1/2}$ against ϕ (Fig. 5A) had its least maximum (i.e., optimal combination between structure and continuity) with 7 classes and $\phi = 1.9$. Moreover, plots of fuzziness performance index (F') and normalized classification entropy (H') against number of classes both revealed local minima at 7 classes (Fig. 5B). Subpopulations on summer range indicated mixed associations among groups (Fig. 6). However, subpopulations adjacent to Deerfield Lake (Fig. 6) had less overlap with other subpopulations.

Kaplan–Meier survival analysis using subpopulation as a covariate identified 2 groups (Table 6). Subpopulations C and G (Fig. 6) had no mortalities and small sample size. Survival analysis using fuzzy-group membership to summer subpopulation C indicated that fuzzy membership was not an important variable explaining individual survival (Table 7). All models incorporating fuzzy membership had high standard errors, indicating poor model fit. Therefore, we did not conduct analysis of habitat characteristics by survival. Deer did not move as subpopulations between summer and winter ranges; 47.9 ± 4.3% of deer that had high membership coefficients on winter ranges were associated on summer ranges.

DISCUSSION

Garshelis (2000) recommended a study design of monitoring habitat use of individuals on one study area comparing use of different habitats to eventual reproduction or survival. We demonstrated a relationship between survivorship on winter range and differential habitat use among subpopulations. Subpopulations with differential habitat use for cover (e.g., large trees) in winter had increased survival. Most previous studies that attempted to measure an association between demographic parameters and habitat use employed animal density (Garshelis 2000; but see Loegering and Fraser 1995; Pettorelli et al. 2003*b*, 2005; Nilsen et al. 2004; McLoughlin et al. 2006). However, density is fraught with difficulties as a measure of demographic fitness (Van Horne 1983 but see Bock and Jones 2004). Garton et al. (2001) concluded that relating demographic response to landscape conditions was the ultimate experimental design for radiotelemetry studies.

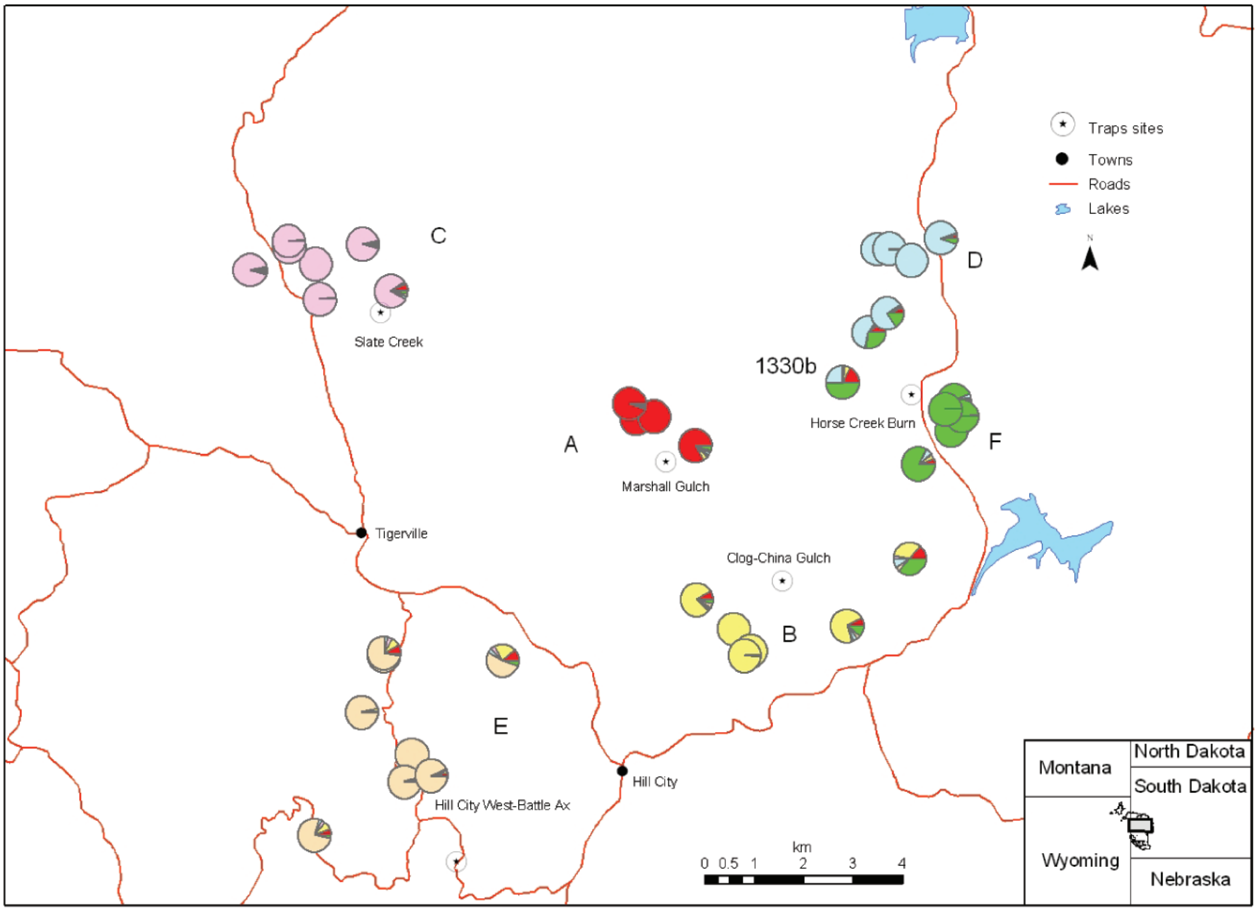


Figure 4. Classification of female white-tailed deer on winter range in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. Pie charts are located at harmonic centers of winter range radio relocations and divisions of pie charts indicate degree of membership of the 6 classes. Subpopulations are labeled A to F.

Fuzzy clustering has been used in several ecological applications including community classification (Roberts 1986, Dayong 1988, Equihua 1990, Nicholls and Tudorancea 2001), soil classification (Odeh et al. 1992), climatic classification (McBratney and Moore 1985), ecosystem analysis (Bosserman and Ragade 1982, Schroeter et al. 1993), population dynamics (Barros et al. 2000), population genetic structure (Schaefer and Wilson 2002), and wildlife habitat analysis (Ayyub and McCuen 1987). Fuzzy-set theory addresses the borderline groups, is an exact approach to handle continuous variation, assigns individuals to classes, and reconciles the need for structure in an ambiguous biological world (Zadeh 1965, Schaefer and Wilson 2002). Schaefer and Wilson (2002) strongly argued that fuzzy classification better represents the post-Darwinian biopopulation view of individuals as opposed to the previous Aristotelian concept of class. Thus, McBratney and Moore (1985) concluded the fuzzy-set approach is more realistic, more flexible, and may provide better information transfer. Nevertheless, random sampling is necessary to ensure the classification reflects biological observations and not sampling design.

Table 3. Results from Kaplan–Meier analysis for the effect of winter subpopulation on individual survivorship for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996.

Model	ΔAIC_c[a]	w_i[b]	K[c]	Deviance
S(A = B = E = F, C = D)	0.0000	0.65796	2	229.4021
S(A = B, C = D, E = F)	2.0114	0.24067	3	229.4019
S(.)	4.0474	0.08696	1	235.4574
S(group)	7.6434	0.01440	6	228.9753

[a] Difference in Akaike's Information Criterion corrected for small sample size (AIC_c) from the best model. AIC_c for the best model was 233.414.
[b] Akaike wt.
[c] No. of parameters.

Spatiotemporal connectedness is important for denoting populations (Mayr 1988, Baum 1998). As described by Equihua (1990), we explored important habitat variables, characterized clusters by subpopulations, and investigated main effects of habitat variables by subpopulation. Fuzzy classification enabled distinct and indistinct classification of individuals on winter and summer range, which were weighted according to degree of membership necessary to characterize deer associations. Similar to Mauritzen at al. (2002) and Nicholson et al. (1997), we combined space use and geographical position to define ecologically relevant spatial population structures. Because the spatial organization arose from site fidelity, rather than focusing simply on trap location, we were able to retain the full spatial

Table 4. Results from Kaplan–Meier analysis for the effect of time and fuzzy membership to winter subpopulation C on individual survivorship for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996.

Model	ΔAIC_c[a]	w_i[b]	K[c]	Deviance
S(month = Apr different + fuzzy membership)	0.0000	0.47996	3	224.4289
S(month = Apr different)	0.8386	0.31558	2	227.2791
S(trend + fuzzy membership)	3.8709	0.06929	3	228.2998
S(trend)	4.6231	0.04757	2	231.0637
S(yr + fuzzy membership)	5.4909	0.03082	5	225.8847
S(fuzzy membership)	6.1078	0.02264	2	232.5483
S(yr)	6.3855	0.01971	4	228.7988
S(.)	7.0090	0.01443	1	235.4574
S(yr × month)	42.7913	0.00000	42	185.5951

[a] Difference in Akaike's Information Criterion corrected for small sample size (AIC_c) from the best model. AIC_c for the best model was 230.452.
[b] Akaike wt.
[c] No. of parameters.

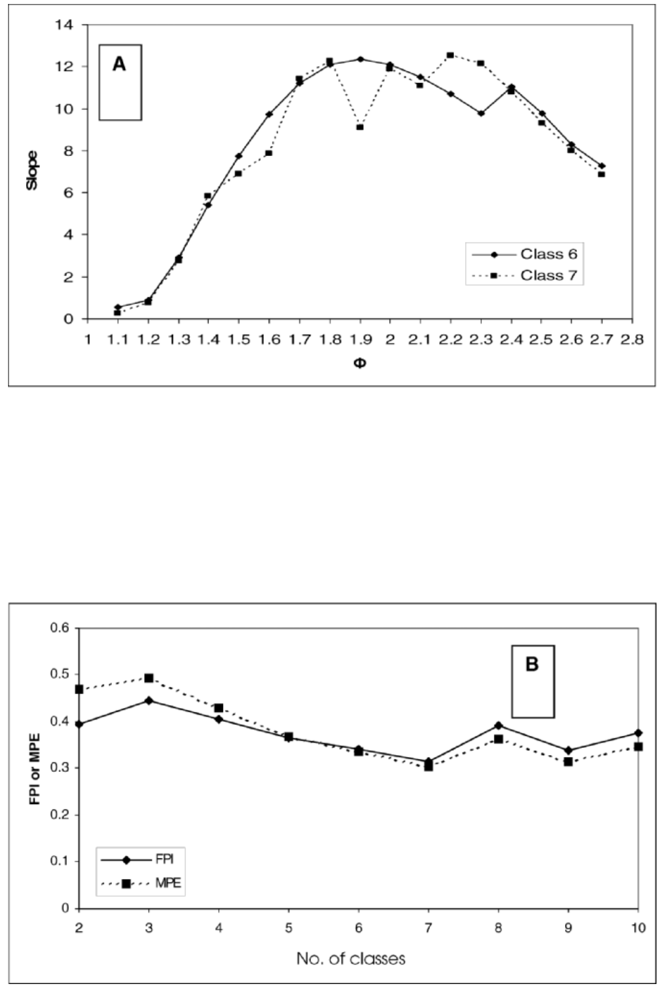


Figure 5. Relationship between the classes and the degree of fuzziness, ϕ, for classification of female white-tailed deer on summer range in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. A) Relationship between slope, $(-\delta J_m/\delta\phi)c^{1/2}$, and ϕ for both 6 and 7 classes. We chose a value of $\phi = 1.9$ because both 6 and 7 classes were a maximum at this value. B) Relationship between fuzziness performance index (FPI) and modified partition entropy (MPE), H', with $\phi = 1.9$. Both FPI and H' indicated local minimum at 7 classes.

resolution of the data and offer a means to dispense with arbitrary demarcations of biological groups (Schaefer and Wilson 2002). Furthermore, we delineated subpopulations based on the spatial affiliations of individuals over several years (Wells and Richmond 1995, Thomas and Kunin 1999, Schaefer et al. 2001).

Similar to caribou (Schaefer et al. 2001), white-tailed deer had high site fidelity on winter range. During winter, females were clumped and tolerant of individuals (Fig. 4). However, prior to fawning, white-tailed deer migrated from winter to summer range (DePerno 1998; DePerno et al. 2002, 2003); subpopulation membership was not associated with survival. Our results indicate no sharp population boundaries on summer range, whereas population units on winter range were significantly segregated from other units.

Table 5. Least-squares means and standard errors of microhabitat variables on white-tailed deer winter range in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996, by survivorship group.

	Survivorship group			
	High		Low	
Variable	$\bar{x}$	SE	$\bar{x}$	SE
Basal area (m^2/ha)	14.8	0.8	13.1	0.9
Dbh (cm)	8.3	0.35	6.7	0.4
Total tall shrubs and saplings (stems/ha)	2,184	390	2,280	434
Coniferous canopy cover (%)	54.08	2.50	51.01	2.78
Deciduous canopy cover (%)	1.51	0.8	1.62	0.9
Total canopy cover (%)	55.6	2.5	52.6	2.7
Grass (%)	3.0	0.2	3.2	0.3
Forbs (%)	9.9	1.3	12.1	1.4
Shrubs (%)	3.8	0.4	4.0	0.4
Slash (%)	4.9	0.3	3.4	0.3
Total point-center quarter distance (m)	2.8	0.1	2.2	0.2
Total visual obstruction low (%)	36.7	2.2	40.0	2.4
Total visual obstruction high (%)	23.9	1.8	24.2	2.0
Total distance to visual obstruction (m)	43.0	2.6	46.0	2.9

Nevertheless, results from the fuzzy classification (Figs. 4, 6), although clumped on winter range and dispersed on summer range, indicated a spatial structuring of the central Black Hills deer population. Spatial structures on summer range were influenced by winter range associations; summer subpopulations averaged 48% membership of winter subpopulations. Deer associated with subpopulations differed in migration patterns and the areas occupied by subpopulations in winter differed in habitat characteristics. Griffin et al. (1999) found the timing of deer migration from winter range was similar among subpopulations. We show that deer from subpopulations did not necessarily move to the same summer range, which differed from our prediction but was comparable to mule deer in Nevada (Gruell and Papez 1963). Nelson and Mech (1987) noted that 95% of deer in their study used summer ranges within the same regions as other deer in winter yards. Lower association (48%) between deer movement from winter to

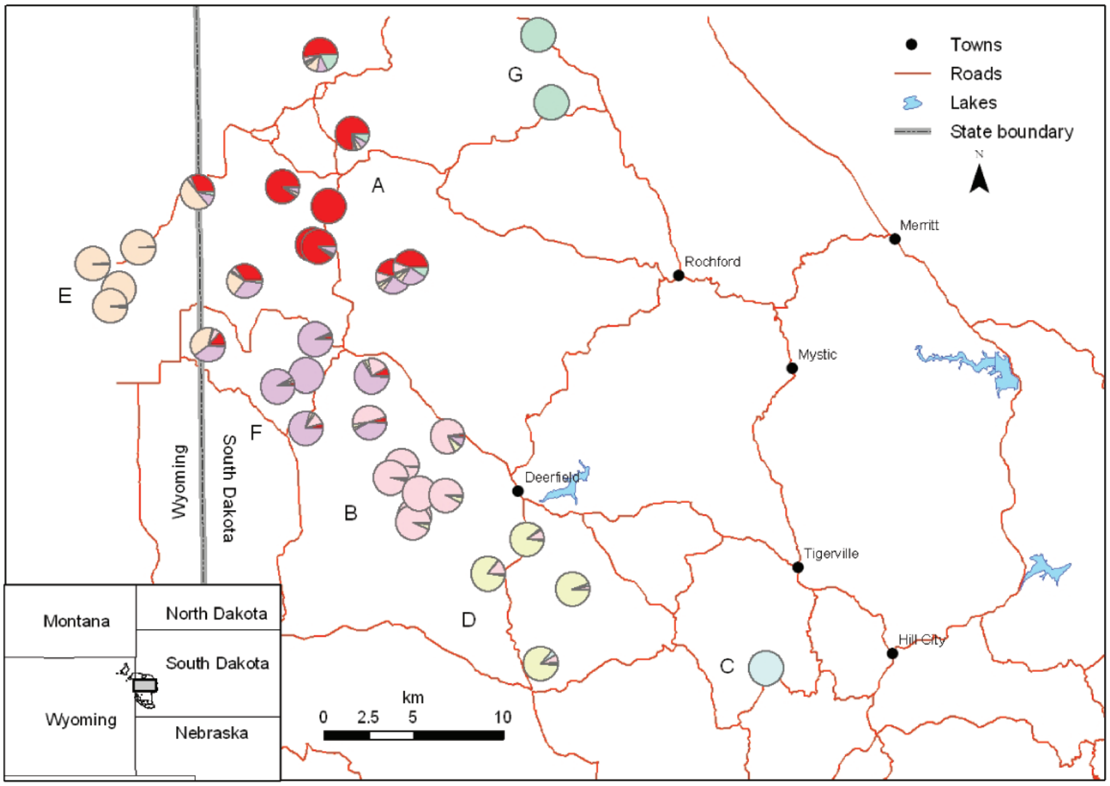


Figure 6. Classification of female white-tailed deer on summer range in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996. Pie charts are located at harmonic centers of summer range radio relocations and divisions of pie charts indicate degree of membership for the 7 classes. Subpopulations are labeled A to G.

specific summer range was likely indicative of patch-size constraints that increased dispersion of deer.

In the central Black Hills, Hippensteel (2000) determined that winter-range diets of deer were composed of 40% ponderosa pine, 30% grass, 20% shrub, and 5% forbs, which supports the contention that poor-quality habitat was present in the region (Sieg and Severson 1996, Osborn and Jenks 1998). The data of Hippensteel (2000) provided strong support for the high fidelity evidenced by clumping behavior and association observed on winter range in the central Black Hills. Quality winter-range habitat was sparse in the central Black Hills and it has been concluded that >90% of forest stands lacked sufficient understory vegetation or tall shrub saplings (DePerno 1998; DePerno et al. 2000, 2002, 2003). Under these conditions, larger trees with associated slash likely allowed adult deer to minimize energy costs by improving thermal conditions (i.e., radiation cover; DePerno et al. 2003).

Similar to other studies, we observed high site fidelity on winter range in the central Black Hills (Figs. 1, 4; Tierson et al. 1985, Griffin et al. 1999, Brinkman 2003, Brinkman et al. 2005). Habitat characteristics associated with cover differed by subpopulation and were related to survival probabilities, which supported our prediction. In winter, 71% of deer mortality was characterized as natural and, thus, was related to habitat conditions (DePerno et al. 2000). High survival was associated with more open forests characterized by larger trees. Because forage conditions in this region were poor during winter, habitats that enhanced survival may have allowed deer to scan for predators while

Table 6. Results from Kaplan–Meier analysis for the effect of summer subpopulation on individual survivorship for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996.

Model	ΔAIC_c[a]	w_i[b]	K[c]	Deviance
S(A = B = D = E = F, C = G)	0.0000	0.54223	2	193.5343
S(.)	1.0179	0.32595	1	196.5602
S(A = C = E = F = G, B = D)	2.9002	0.12718	2	196.4345
S(group)	9.5240	0.00464	7	192.9587

[a] Difference in Akaike's Information Criterion corrected for small sample size (AIC_c) from the best model. AIC_c for the best model was 197.546.
[b] Akaike wt.
[c] No. of parameters.

Table 7. Results from Kaplan–Meier analysis for the effect of time and fuzzy membership to summer subpopulation C on individual survivorship for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, USA, 1993–1996.

Model	ΔAIC_c[a]	w_i[b]	K[c]	Deviance
S(yr)	0.0000	0.50322	4	178.5095
S(trend)	0.3142	0.43006	2	182.8517
S(.)	4.0410	0.06672	1	188.5864
S(yr × month)	46.1476	0.00000	42	144.9578

[a] Difference in Akaike's Information Criterion corrected for small sample size (AIC_c) from the best model. AIC_c for the best model was 186.550.
[b] Akaike wt.
[c] No. of parameters.

occupying sites with positive thermal benefits (DePerno et al. 2003). We found no association between habitat characteristics and survival in summer, contrary to our prediction. Thus, habitat characteristics in summer may be more related to survival of offspring than of adults.

Identifying population and subpopulation borders is critical to understanding ecology and dynamics of animal populations (See Bethke et al. 1996, Baguette et al. 2000, Taylor et al. 2001, Mauritzen et al. 2002). For migratory animals where levels of sustainable harvest are based on demographic parameters, small errors may have long-term consequences (Bethke et al. 1996, Nicholson et al. 1997). Furthermore, in seasonally migrating species, spatial population structure may be seasonally dependent and temporally dynamic (see Bowen 1997, Mauritzen et al. 2002). Use of fuzzy clustering allowed a detailed description of geographic patterns in space use that were correlated with resource use and survival of deer.

MANAGEMENT IMPLICATIONS

Movement, home range, and habitat relationships of white-tailed deer populations were important to long-term maintenance. In the Black Hills, fuzzy clustering classified winter range into 6 subpopulations primarily corresponding to capture location and indicated that site fidelity of deer was high. Hence, small-scale forest modifications could impact significant segments of this population both positively and negatively. For example, deer using the burn-pine vegetation type from the 1939 McVey fire were classified into a different subpopulation than adjacent deer from the same trapsite. Deer from the McVey fire were in the high-survivorship group, while the adjacent deer were in the lower survivorship group. Use of prescribed burns would benefit winter range for these deer, as noted by Sieg and Severson (1996). Currently, winter range in the central Black Hills is managed uniformly. Based on subpopulation effects, we recommend winter range in the central Black Hills be managed using a fine-scale approach. In winter, habitat characteristics that enhanced survival probabilities included relatively high basal area, diameter at breast height of trees, cover of slash, and distance among trees. Habitat manipulations that promote or maintain large trees (i.e., basal area = 14.8 m^2/ha and average dbh of trees = 8.3 cm) would seem to improve adult survival of deer in winter.

ACKNOWLEDGMENTS

Our study was supported by Federal Aid to Wildlife Restoration Project W-75-R (Study No. 7563 and 7564) administered through South Dakota Department of Game, Fish, and Parks. D. Beck, B. Bol, S. Clark, D. Flory, B. A. Hippensteel, D. Knowlton, and J. McCormick assisted with field work. We gratefully acknowledge critical reviews of the manuscript that improved previous versions by P. E. Bartelt, D. M. Fecske, J. R. Fieberg, A. L. Gallant, J. Giudice, J. A. Schaefer, and anonymous reviewers. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government.

LITERATURE CITED

Ayyub, B. M., and R. H. McCuen. 1987. Quality and uncertainty assessment of wildlife habitat and fuzzy sets. Journal of Water Resources Planning and Management 113:95–109.

Baguette, M., S. Petit, and F. Queva. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. Journal of Applied Ecology 37:100–108.

Barros, L. C., R. C. Bassanezi, and P. A. Tonelli. 2000. Fuzzy modeling in population dynamics. Ecological Modeling 128:27–33.

Baum, D. A. 1998. Individuality and the existence of species through time. Systematic Biology 47:641–653.

Bethke, R., M. Taylor, S. Amstrup, and F. Messier. 1996. Population delineation of polar bears using satellite collar data. Ecological Applications 6:311–317.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403–410.

Bosserman, R. W., and R. K. Ragade. 1982. Ecosystem analysis using fuzzy set theory. Ecological Modeling 16:191–208.

Bowen, B. W. 1997. Complex population structure and the conservation genetics of migratory marine mammals: lessons from sea turtles. Pages 77–84 *in* A. E. Dizon, S. J. Chivers, and W. F. Perrin, editors. Molecular genetics of marine mammals. Special Publication No. 3. The Society for Marine Mammalogy, Lawrence, Kansas, USA.

Bowyer, R. T. 1986. Habitat selection by southern mule deer. California Fish and Game 72:153–169.

Brinkman, T. J. 2003. Movement and mortality of white-tailed deer in southwest Minnesota. Thesis, South Dakota State University, Brookings, USA.

Brinkman, T. J., C. S. DePerno, J. A. Jenks, and B. S. Haroldson. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. Journal of Wildlife Management 69:1099–1111.

Brown, D. G. 1998. Mapping historical forest types in Baraga County Michigan, USA as fuzzy sets. Plant Ecology 134:97–111.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Clover, M. R. 1956. Single gate deer trap. California Fish and Game 40: 199–201.

Clutton-Brock, T. H., and P. H. Harvey. 1978. Mammals, resources, and reproductive strategies. Nature 273:191–195.

Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. American Statistician 35:124–129.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology 78:852–863.

Coulson, T., S. D. Albon, J. Pilkington, and T. H. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. Journal of Animal Ecology 68:658–671.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

Dayong, Z. 1988. An index to measure the strength of relationship between community and site. Ecological Modeling 40:145–153.

D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736–744.

DePerno, C. S. 1998. Habitat selection of a declining white-tailed deer herd in the central Black Hills, South Dakota and Wyoming. Dissertation, South Dakota State University, Brookings, USA.

DePerno, C. S., S. L. Griffin, J. A. Jenks, and L. A. Rice. 1997. An unusual migration by a white-tailed deer fawn. The Prairie Naturalist 29:93–97.

DePerno, C. S., J. A. Jenks, and S. L. Griffin. 2003. Multidimensional cover characteristics: is variation in habitat selection related to white-tailed deer sexual segregation? Journal of Mammalogy 84:1316–1329.

DePerno, C. S., J. A. Jenks, S. L. Griffin, and R. W. Klaver. 2001. Use of the USDA Forest Service geographic information system for determining cover type use by white-tailed deer. Proceedings of the South Dakota Academy of Science 80:201–211.

DePerno, C. S., J. A. Jenks, S. L. Griffin, and L. A. Rice. 2000. Female survival rates in a declining white-tailed deer population. Wildlife Society Bulletin 28:1030–1037.

DePerno, C. S., J. A. Jenks, S. L. Griffin, L. A. Rice, and K. F. Higgins. 2002. White-tailed deer habitats in the central Black Hills. Journal of Range Management 55:242–252.

Equihua, M. 1990. Fuzzy clustering of ecological data. Journal of Ecology 78:519–534.

Focardi, S., E. R. Pelliccioni, R. Petrucco, and S. Toso. 2002. Spatial patterns and density dependence in the dynamics of a roe deer (*Capreolus capreolus*) population in central Italy. Oecologia 130:411–419.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–64 *in* L. Boitanti and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 13–42 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Griffin, S. L., C. S. DePerno, J. A. Jenks, L. A. Rice, and D. A. Flory. 1995. Capture success of white-tailed deer in the central Black Hills, South Dakota. Proceedings of the South Dakota Academy of Science 74: 71–76.

Griffin, S. L., L. A. Rice, C. S. DePerno, and J. A. Jenks. 1999. Seasonal movements and home ranges of white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993-1997. Pitman-Robertson Project W-75-R-34 Completion Report No. 99-03. South Dakota Department of Game, Fish, and Parks, Pierre, USA.

Gruell, G. E., and N. J. Papez. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Management 27:414–422.

Hayes, C. L., and P. R. Krausman. 1993. Nocturnal activity of female desert mule-deer. Journal of Wildlife Management 57:897–904.

Hilden, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2: 53–75.

Hippensteel, B. A. 2000. Nutritional condition of white-tailed deer in the central Black Hills, South Dakota: influence of habitat and elk competition. Thesis, South Dakota State University, Brookings, USA.

Hovind, H. J., and C. E. Reick. 1970. Basal area and point sampling: interpretation and application. Wisconsin Department of Natural Resources Technical Bulletin 23:1–52.

Kernohan, B. J., J. A. Jenks, D. E. Naugle, and J. J. Millspaugh. 1996. Estimating 24-h habitat use patterns of white-tailed deer from diurnal use. Journal of Environmental Management 48:299–303.

Kirsch, E. M. 1996. Habitat selection and productivity of least terns in the lower Platte River, Nebraska. Wildlife Monographs 132.

Klaver, R. W. 2001. Effects of scale on habitat selection of female white-tailed deer in the central Black Hills, South Dakota and Wyoming. Dissertation, South Dakota State University, Brookings, USA.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314–320.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Loegering, M. V., and J. D. Fraser. 1995. Factors affection piping plover chick survival in different brooding-rearing habitats. Journal of Wildlife Management 59:329–335.

Marsili-Libelli, S. 1989. Fuzzy clustering of ecological data. Coenoses 4: 95–106.

Mauritzen, M., A. E. Derocher, O. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. Journal of Applied Ecology 39:79–90.

Mayr, E. 1988. Toward a new philosophy of biology. Belknap Press, Cambridge, Massachusetts, USA.

McBratney, A. B., and A. W. Moore. 1985. Application of fuzzy sets to climatic classification. Agricultural and Forest Meteorology 35:165–185.

McLoughlin, P. D., M. S. Boyce, T. Caulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent multivariable resource selection. Proceedings of the Royal Society Series B 273:1449–1454.

McLoughlin, P. D., H. D. Cluff, R. J. Gau, R. Mulders, R. L. Case, and F. Messier. 2002. Population delineation of barren-ground grizzly bears in the central Canadian Arctic. Wildlife Society Bulletin 30:728–737.

Millsapugh, J. J., and J. M. Marzluff. 2001. Radio-tagging and animal populations: past trends and future needs. Pages 383–393 *in* J. J. Millsapugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Minasny, B., and A. B. McBratney. 2002. FuzME version 3.0. Australian Centre for Precision Agriculture, The University of Sydney, Australia. <http://www.usyd.edu.au/su/agric/acpa>. Accessed 10 Jan 2005.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife–habitat relationships: concepts and applications. Second edition. University of Wisconsin Press, Madison, USA.

Neft, D. S. 1966. Statistical analysis for areal distributions. Regional Science Research Institute, Philadelphia, Pennsylvania, USA.

Nelson, M. E., and L. D. Mech. 1987. Demes within a northeastern Minnesota deer population. Pages 27–40 *in* B. D. Chepko-Sade and C. T. Halpin, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

Nicholls, K. H., and C. Tudorancea. 2001. Application of fuzzy cluster analysis to Lake Simcoe crustacean zooplankton community structure. Canadian Journal of Zoology 58:231–240.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Nilsen, E. B., J. D. Linnell, and R. Andersen. 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. Journal of Animal Ecology 73:44–50.

Odeh, I. O. A., A. B. McBratney, and D. J. Chittleborough. 1992. Soil pattern recognition with fuzzy-c-means: application to classification and soil–landform interrelationships. Soil Science Society of America Journal 56:505–516.

Osborn, R. G. 1994. Winter diet and nutritional condition of white-tailed deer in the northern Black Hills, South Dakota. Thesis, South Dakota State University, Brookings, USA.

Osborn, R. G., and J. A. Jenks. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. Journal of Mammalogy 79:437–447.

Pettorelli, N., S. Dray, J.-M. Gaillard, D. Chessel, P. Ducan, A. Illius, N. Guillon, F. Klein, and G. Van Laere. 2003*a*. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. Oecologia 137:363–369.

Pettorelli, N., J.-M. Gaillard, P. Duncan, D. Maillard, G. Van Laere, and D. Delorme. 2003*b*. Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology 84:3307–3316.

Pettorelli, N., J.-M. Gaillard, N. G. Yoccoz, P. Duncan, D. Maillard, D. Delorme, G. Van Laere, and C. Toïgo. 2005. The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. Journal of Animal Ecology 74:972–981.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Roberts, D. W. 1986. Ordination on the basis of fuzzy set theory. Vegetatio 66:123–131.

Schaefer, J. A., A. M. Veitch, F. H. Harrington, W. K. Brown, J. B. Theberge, and S. N. Luttich. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. Oecologia 126:507–514.

Schaefer, J. A., and C. C. Wilson. 2002. The fuzzy structure of populations. Canadian Journal of Zoology 80:2235–2241.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367–374.

Schroeter, S. C., J. D. Dixon, J. Kastendiek, and R. O. Smith. 1993.

Detecting the ecological effects of environmental impacts: a case study of kelp forest invertebrates. Ecological Applications 3:331–350.
Sieg, C. H., and K. E. Severson. 1996. Managing habitats for white-tailed deer. Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. U.S. Department of Agriculture Forest Service, General Technical Report RG-GTR-274. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
Smith, V. J., J. A. Jenks, C. R. Berry, Jr., C. J. Kopplin, and D. M. Fecske. 2002. The South Dakota Gap Analysis Project. Final report. Research work order No. 65. Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, USA.
Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, United Kingdom.
Svärdson, G. 1949. Competition and habitat selection in birds. Oikos 1: 157–174.
Taylor, M. K., S. Akeeagok, D. Andriashek, W. Barbour, E. W. Born, W. Calvert, H. D. Cluff, S. Ferguson, J. Laake, A. Rosing-Asvid, I. Stirling, and F. Messier. 2001. Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. Canadian Journal of Zoology 79:690–709.
Thilenius, J. F. 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. U.S. Department of Agriculture Forest Service, research paper RM-91. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology 68:647–657.
Tierson, W. C., G. F. Mattfield, R. W. Sage, Jr., and D. F. Behrend. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. Journal of Wildlife Management 49:760–769.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
Wells, J. V., and M. E. Richmond. 1995. Populations, metapopulations, and species populations: what are they and who should care? Wildlife Society Bulletin 23:458–462.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.
Zadeh, L. A. 1965. Fuzzy sets. Information and Control 8:338–363.
Zannèse, A., N. Morellet, C. Targhetta, A. Coulon, S. Fuser, A. J. M. Hewison, and M. Ramanzin. 2006. Spatial structure of roe deer populations: towards defining management units at a landscape scale. Journal of Applied Ecology 43:1087–1097.

Associate Editor: Hudson.