

MULTIDIMENSIONAL COVER CHARACTERISTICS: IS VARIATION IN HABITAT SELECTION RELATED TO WHITE-TAILED DEER SEXUAL SEGREGATION?

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We documented cover characteristics at white-tailed deer (*Odocoileus virginianus dakotensis*) bedding and feeding sites on winter and summer ranges in the central Black Hills, South Dakota and Wyoming. Radiolocations of female (2,592; $n = 73$) and male (573; $n = 12$) deer were compared with 1,087 random locations. Characteristics of cover recorded at deer and random locations included basal area, point-centered quarter distance, density of tall shrubs and saplings, and available hiding (horizontal) cover. On winter range, females selected areas with lower levels of hiding cover than males, whereas habitats selected on summer range were similar. On winter and summer ranges, females bedded in areas with greater hiding cover than feeding or random sites. Three principal components (interpreted as hiding cover, thermal cover, and radiation cover) differed with respect to season and explained 78.5% of the variation in cover characteristics. In winter, males had higher scores for hiding cover, while females had higher scores for radiation cover. Conversely, during summer, females had higher scores for hiding and thermal cover. Results were compared to the reproductive-strategy (RSH) and predator-avoidance (PAH) hypotheses, which attempt to explain sexual segregation in ungulates. Univariate results indicated the sexes occupied habitats with similar cover characteristics on summer range but not on winter range. Therefore, we rejected the RSH for summer range but were unable to reject the RSH for winter range. Also, hiding cover was of greater importance to males on winter range and females on summer range. Based on these results, we rejected the PAH for winter range but were unable to reject the PAH for summer range.

Key words: Black Hills, hiding cover, *Odocoileus virginianus dakotensis*, predator-avoidance hypothesis, reproductive-strategy hypothesis, resource partitioning, sexual segregation, South Dakota, white-tailed deer, Wyoming

Characteristics of cover may explain how resources are partitioned between sexes and how habitat choices benefit male and female white-tailed deer (*Odocoileus virginianus*). Hiding cover is represented by density of understory vegetation <1 m in height and may include vegetation charac-

teristics, such as density of tall shrubs and saplings, basal area, and tree diameter. In addition, thermal (Parker and Gillingham 1990) and radiation (Moen 1976) properties of cover can influence selection of microsites by animals. Understory vegetation may provide relief from weather (Parker and Gillingham 1990), a means with which to escape predators (King and Smith 1980),

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and forage (Bowyer et al. 1999; Kie and Bowyer 1999). The original objectives of this study were to document characteristics of hiding cover at bedding and feeding sites on winter and summer ranges for male and female white-tailed deer and to compare these locations with random sites. We believed, however, the data were appropriate for examining hypotheses related to seasonal sexual segregation (Kie and Bowyer 1999).

Numerous hypotheses exist to explain the presence of resource partitioning and sexual segregation in ungulates (Bleich 1993; Bleich et al. 1997; Geist and Petocz 1977; Main and Coblenz 1990, 1996; Miquelle et al. 1992). However, 2 major hypotheses predominate. The reproductive-strategy hypothesis (RSH) predicts that males and females should use habitats differently to increase reproductive fitness (Bleich 1993; Bleich et al. 1997; Geist and Petocz 1977; Main and Coblenz 1990; Main et al. 1996; Miquelle et al. 1992; Weckerly 1993). Geist and Petocz (1977) proposed that, by remaining near the female and young, males could reduce growth and development of their offspring by depriving them of resources, could impair the physiological condition of females for the next season, and risk underdevelopment and mortality of their future offspring. The predator-avoidance hypothesis (PAH) suggests that spatial separation of the sexes occurs because mature males are less susceptible to predators than smaller females and young (Bleich 1993; Bleich et al. 1997; Geist 1982). This hypothesis is based on females selecting areas that provide adequate food, water, and security to raise offspring even if this precludes exploiting superior forage opportunities (Main and Coblenz 1990). Whereas mature males, by way of their greater freedom of movement, differentially use high-predation areas to maximize nutrient intake (Bleich 1993; Bleich et al. 1997; Festa-Bianchet 1988; Geist 1982; King and Smith 1980; Main and Coblenz 1990, 1996; McCullough et al. 1989). By using habitats

differently, males are able to maximize nutrient intake (Festa-Bianchet 1988; Geist 1982; King and Smith 1980; Main and Coblenz 1990; McCullough et al. 1989) while females and young minimize risk of predation (Ober 1931).

We discuss the ramifications of cover characteristics relative to the RSH and the PAH separately for winter and summer ranges. We hypothesized that females migrate from winter to summer range to give birth in areas that provide thermal cover, maximum forage characteristics, and concealment cover for fawns, whereas males are migrating to sites on summer range with maximum forage characteristics to maximize body condition.

STUDY AREA AND METHODS

The Black Hills is an isolated mountainous area in western South Dakota and northeast Wyoming. The central Black Hills study area has been described previously (DePerno 1998; DePerno et al. 2000, 2001, 2002; Griffin et al. 1995, 1999). Elevation ranges from 973 to 2,202 m above mean sea level (Orr 1959; Turner 1974). Annual temperatures are typical of a continental climate and range from 5 to 9°C with extremes of -40 and 44°C, and mean annual precipitation ranges from 45 to 66 cm and yearly snowfall may exceed 254 cm at higher elevations (Orr 1959; Thilenius 1972).

The central Black Hills study area (43°52'N to 44°15'N, 104°07'W to 103°22'W) was composed of separate winter and summer ranges used by migratory white-tailed deer (DePerno 1998; Griffin et al. 1995, 1999) and included Pennington and Lawrence Counties of South Dakota and Crook and Weston counties of Wyoming (Fig. 1). Public land within the study area was managed by the United States Department of Agriculture Forest Service primarily for timber production and livestock grazing between 1 June and 31 October. Mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and dogs are primary predators of deer in this region. In the central Black Hills, coyotes were responsible for 34% (15/44) of female mortalities, whereas coyotes were responsible for 11% (1/9) of male mortalities (DePerno et al. 2000). Similarly, annual mortality of fawn

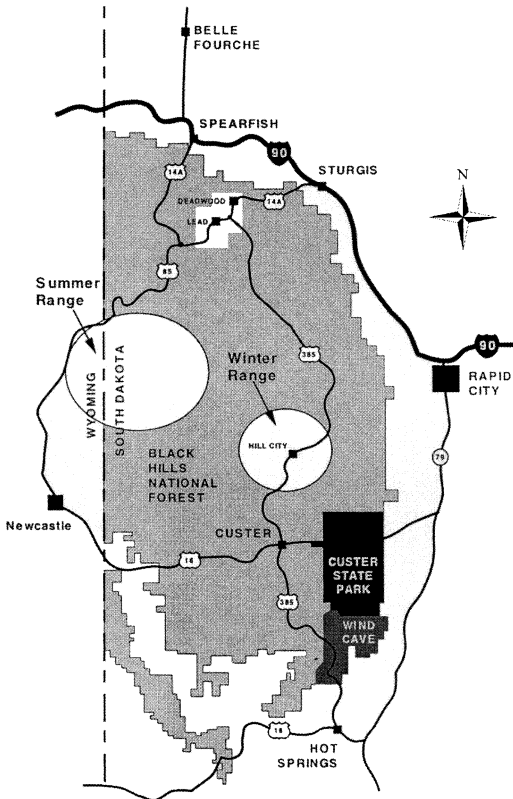


FIG. 1.—Locations of winter and summer ranges of white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

white-tailed deer in the central Black Hills was 70% with predation (bobcat, coyote) accounting for 60% of all mortalities (Benzon 1998).

Overstory vegetation on winter range consisted of ponderosa pine (*Pinus ponderosa*) interspersed with small stands of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*)—Hoffman and Alexander 1987; McIntosh 1949; Richardson and Petersen 1974; Thilenius 1972). Understory vegetation on winter range included snowberry (*Symphoricarpos albus*), spiraea (*Spiraea betulifolia*), serviceberry (*Amelanchier alnifolia*), woods rose (*Rosa woodsii*), bearberry (*Arctostaphylos uva-ursi*), and cherry (*Prunus*). Overstory vegetation on summer range was dominated by stands of ponderosa pine and white spruce (*Picea glauca*) interspersed with small stands of quaking aspen (Hoffman and Alexander 1987; McIntosh 1949; Richardson and Petersen 1974; Thilenius 1972). Understory vegetation on summer range was

represented by Oregon grape (*Berberis repens*), juniper (*Juniperus communis*), bearberry, snowberry, spiraea, and serviceberry.

We captured 480 white-tailed deer in February and March 1993–1996 (Griffin et al. 1995, 1999) using modified, single-gate Clover traps (Clover 1956) baited with fresh alfalfa hay. We captured deer on 4 trap sites located northeast, northwest, and west of Hill City, South Dakota, on the McVey Burn deer winter range (DePerno 1998; DePerno et al. 2000, 2001, 2002; Griffin et al. 1995, 1999). Adult and yearling female ($n = 73$) and male ($n = 12$) white-tailed deer were fitted with radiocollars (Telonics Inc., Mesa, Arizona; Lotek Engineering, Inc. Ontario, Canada), were ear-tagged, had their age estimated based on incisor wear, and were released. An Institutional Animal Care and Use Committee at South Dakota State University approved all methods used in this research.

From July 1993 through July 1996, individual radiocollared deer were visually located from the ground, 1–3 times per week. Deer were radiotracked at different time periods during the day to maximize observations of diurnal activities (Hayes and Krausman 1993; Kernohan et al. 1996) and to obtain adequate sample sizes without violating the assumption of independent observations (White and Garrott 1990). Hayes and Krausman (1993) and Kernohan et al. (1996) demonstrated no differences between diurnal and 24-h habitat use for mule deer and white-tailed deer, respectively.

Each radiocollar used in this study contained a mercury tip switch that enabled determination of head-up and head-down position based on signal intensity and differing pulse intervals (Beier and McCullough 1988). Activity (feeding and bedding) was determined by radiosignal intensity, speed of the pulse intervals (Beier and McCullough 1988; Hansen et al. 1992; Weckerly 1993), and visual confirmation. Deer locations were plotted on 7.5-min United States Geological Survey topographical maps (scale, 1:24,000) and assigned Universal Transverse Mercator (UTM) coordinates (Edwards 1969; Grubb and Eakle 1988).

Separate winter and summer ranges were used by migratory white-tailed deer in the Black Hills (DePerno 1998; DePerno et al. 2000, 2001, 2002; Griffin et al. 1995, 1999). Therefore, we stratified data according to seasonal elevation shifts made by each individual each year (Apps

et al. 2001) and classified each deer location and the corresponding habitat information as either winter or summer range. Habitat information was collected from a 400-m² circular plot centered on each deer observation site (providing the location of the radiocollared deer was visually determined without disturbing the animal) and from computer-generated random locations (DePerno 1998; DePerno et al. 2002; Kennedy 1992; Marcum and Loftsgaarden 1980). Characteristics of hiding cover recorded at each feeding, bedding, and random location included basal area, tree diameter measured at breast height (DBH), point-centered quarter distance of trees, density of tall shrubs and saplings, and percentage available hiding cover. Basal area, the cross-sectional area of trees, was determined from plot center using a 10-factor angle gauge (Hovind and Rieck 1970) and DBH of each tree included in the basal area count was measured 1.37 m above the ground. Point-centered quarter distance, the distance from plot center to the nearest basal area tree in each of the 4 directional quadrants, was measured with a flexible metric tape (Cottam and Curtis 1956). For analytical purposes, the 4 point-centered quarter distances were averaged for each location.

Density of tall shrubs and saplings, the numbers of shrub or tree saplings present that were >1 m in height and <5 cm DBH (modified from Stauffer and Peterson 1985), were counted along 2 perpendicular, 1-m-high by 1-m-wide by 20-m-long transects oriented north-south and east-west that intersected at plot center. Density of tall shrubs and saplings present was determined separately for saplings <3-cm DBH and saplings with a DBH of 3–5 cm. For analytical purposes, density of tall shrubs and saplings were averaged over the 2 transects.

Vertical screening cover available to deer was evaluated using a 1-m² visual obstruction cloth (DePerno 1998; Kennedy 1992). The cloth, designed in a black and white checkerboard layout, was divided into one hundred 10-cm squares and separated into 2 sections; the bottom 50 squares (0.0–0.5 m) were considered representative of the cover available to a bedded deer, and the top 50 squares (0.5–1.0 m) were considered representative of the cover available to a standing deer (Bowyer 1986). The cloth was secured perpendicular to the ground and 4 readings, 1 from each of the 4 cardinal directions, were made from a distance of 10 m from plot center and 1

m above the ground. A square $\geq 50\%$ covered by vegetation was considered concealed, whereas a square <50% covered by vegetation was considered open. Number of squares concealed, in each of the 2 sections, represented the amount of hiding cover available to bedding and standing deer, respectively. Additionally, the distance at which the visual obstruction cloth was 90% concealed was estimated for each of the 4 cardinal directions (DePerno 1998; Kennedy 1992). For analytical purposes, the 4 visual obstruction percentages and distances were averaged at each location.

Habitat data collected from individual deer were pooled across years, activities, and seasons to compare characteristics of hiding cover. Locations by sex and season were analyzed using analysis of variance (ANOVA). Pearson's correlation coefficients were used to determine significant relationships between hiding cover variables. When pairs of variables were significantly correlated, 1 variable was removed from the data matrix. Orthogonal contrasts were conducted on the remaining variables to compare differences between feeding and bedding and between feeding, bedding, and random locations within sex and season. Activity between sexes within seasons was compared with available habitat using a multivariate analysis of variance (MANOVA). A principal component analysis with varimax rotation of factors (Jenks et al. 1996; Johnson and Wichern 1988) was conducted on the remaining variables in the model as determined by Pearson's correlation. MANOVA was used to evaluate differences in principal component scores (by activity, season, and sex). All analyses were performed using SYSTAT (Wilkinson 1990). Statistical comparisons were considered significant at $P \leq 0.05$. Data are presented as mean \pm SE.

RESULTS

Deer migrated from winter range to summer range in a northwesterly direction. Peak spring migration for females occurred during May, prior to parturition, whereas autumn migration primarily occurred during November (DePerno 1998; DePerno et al. 2000, 2001, 2002; Griffin et al. 1995, 1999). Mean elevations at deer locations on summer range (1,980.3 m; $n = 2,395$) were greater ($F = 15,187.8$, $d.f. = 1, 4,658$, $P <$

0.001) than at deer locations on winter range (1,639.3 m; $n = 2,265$).

Between July 1993 and July 1996, we recorded 2,592 radiolocations for female white-tailed deer. Between February 1994 and July 1996, we recorded 573 radiolocations for male white-tailed deer. However, because of our strict requirements for collecting habitat data (exact location and activity of each animal had to be determined prior to visual disturbance), only 701 locations of females and 54 locations of males contained hiding-cover information at feeding and bedding sites. Excluded from analyses were 1 radiocollared male that remained on winter range throughout the year and 1 radiocollared female that demonstrated an abnormal migration pattern (DePerno et al. 1997). To obtain a measure of habitat available to white-tailed deer, 1,087 (winter range, $n = 528$; summer range, $n = 559$) computer-generated random locations were sampled throughout the study. Prior to conducting principal component analyses, Pearson's correlations were used ($P > 0.355$), which reduced the multivariate model from 9 to 5 variables that explained unique variation within the data, including basal area, average DBH, density of tall shrubs and saplings, high visual obstruction, and distance to complete visual obstruction.

On winter range, female white-tailed deer selected areas with lower density of tall shrubs and saplings (<3 cm, $F = 6.0$, $d.f. = 1, 751$, $P = 0.014$; 3–5 cm, $F = 22.0$, $d.f. = 1, 751$, $P \leq 0.001$), density of tall shrubs and saplings ($F = 9.5$, $d.f. = 1, 751$, $P = 0.002$), and percentage visual obstruction (0–0.5 m, $F = 16.9$, $d.f. = 1, 750$, $P \leq 0.001$; 0.5–1.0 m, $F = 11.4$, $d.f. = 1, 750$, $P \leq 0.001$) than at locations selected by males (Table 1). Additionally, basal area measurements tended to be lower at locations selected by females than males ($F = 2.8$, $d.f. = 1, 1,422$, $P = 0.092$), whereas distance to complete visual obstruction tended to be lower at locations selected by males than females ($F = 6.4$, $d.f. = 1, 750$,

TABLE 1.—Hiding cover variables collected at white-tailed deer locations on winter and summer ranges in the central Black Hills, South Dakota and Wyoming, 1993–1996.

	Winter locations			Summer locations		
	Females $n = 287^a$	Males $n = 27^a$	P	Females $n = 41^a$	Males $n = 27^a$	P
	$\bar{X} \pm SE$	$\bar{X} \pm SE$		$\bar{X} \pm SE$	$\bar{X} \pm SE$	
Basal area (m ² /ha)	13.5 ± 0.5 ^b	16.0 ± 1.4 ^c	0.092	15.7 ± 0.3 ^d	16.4 ± 1.0 ^e	0.489
Average DBH (cm)	7.4 ± 0.2 ^b	7.4 ± 0.6 ^c	0.941	9.1 ± 0.1 ^d	8.5 ± 0.4 ^e	0.165
Density of tall shrubs and saplings (stems/ha)	2,059.2 ± 305.6	5,268.5 ± 997.7	0.002	2,948.1 ± 254.4	3,000.0 ± 996.2	0.960
High visual obstruction (%; 0.5–1.0 m)	21.4 ± 1.5	39.1 ± 5.0	0.001	45.0 ± 1.3	49.0 ± 5.0	0.436
Distance to complete visual obstruction (m)	45.6 ± 1.4	33.9 ± 4.5	0.012	24.8 ± 1.1	25.9 ± 4.4	0.810

^a n for variables not identified by another letter.
^b $n = 471$.
^c $n = 47$.
^d $n = 808$.
^e $n = 100$.

$P = 0.012$). Conversely, on summer range, only density of tall shrubs and saplings (3–5 cm) differed between the sexes ($F = 4.8$, $d.f. = 1, 751$, $P = 0.029$); sapling densities were higher for sites occupied by males than females (Table 1).

On winter range, females bedded in areas that were characterized by greater hiding cover than feeding and random sites (Table 2). Density of tall shrubs and saplings ($F = 10.4$, $d.f. = 1, 811$, $P \leq 0.001$), percentage high visual obstruction ($F = 9.8$, $d.f. = 1, 811$, $P = 0.002$), and distance to complete visual obstruction ($F = 9.4$, $d.f. = 1, 811$, $P = 0.002$) differed between feeding, bedding, and random locations; density of tall shrubs and saplings and percentage high visual obstruction were greater at bedding than at feeding and random sites, while distance to complete visual obstruction was greater at feeding than at bedding and random locations. Similarly, basal area ($F = 44.5$, $d.f. = 1, 811$, $P \leq 0.001$), density of tall shrubs and saplings ($F = 8.8$, $d.f. = 1, 811$, $P \leq 0.003$), and percentage high visual obstruction ($F = 35.9$, $d.f. = 1, 811$, $P \leq 0.001$) were greater at bedding than at feeding locations (Table 2). Average DBH ($F = 4.6$, $d.f. = 1, 811$, $P = 0.032$) and distance to complete visual obstruction ($F = 27.6$, $d.f. = 1, 811$, $P \leq 0.001$) were greater at feeding than at bedding locations (Table 2).

On summer range, basal area ($F = 19.0$, $d.f. = 1, 970$, $P \leq 0.001$), average DBH ($F = 7.5$, $d.f. = 1, 970$, $P = 0.006$), density of tall shrubs and saplings ($F = 35.8$, $d.f. = 1, 970$, $P \leq 0.001$), percentage visual obstruction (0.5–1.0 m; $F = 90.5$, $d.f. = 1, 970$, $P \leq 0.001$), and distance to complete visual obstruction ($F = 46.6$, $d.f. = 1, 970$, $P \leq 0.001$) differed for females between feeding, bedding, and random locations; basal area, density of tall shrubs and saplings, and percentage visual obstruction were greater at bedding than at feeding and random sites, while average DBH and distance to complete visual obstruction were greater at feeding than at bedding and random locations (Table 3). Basal area ($F =$

TABLE 2.—Hiding cover variables collected at white-tailed deer feeding, bedding, and random locations on winter range in the central Black Hills, South Dakota and Wyoming, 1993–1996. Orthogonal contrasts were conducted to compare differences between feeding, bedding, and random locations^a and differences between feeding and bedding locations^b within sex and season.

	Winter locations of males			Winter locations of females		
	Feeding	Bedding	Randoms	Feeding	Bedding	Randoms
	$n = 8$	$n = 19$	$n = 528$	$n = 164$	$n = 122$	$n = 528$
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Basal area (m ² /ha)	16.1 ± 3.2	15.5 ± 2.1	13.3 ± 0.4	9.8 ± 0.7 ^b	17.1 ± 0.8 ^b	13.3 ± 0.4
Average DBH (cm)	9.1 ± 1.5	7.2 ± 1.0	8.2 ± 0.2	8.3 ± 0.3 ^b	7.2 ± 0.4 ^b	8.2 ± 0.2
Density of tall shrubs and saplings (stems/ha)	1,187.5 ± 1,682.2 ^{ab}	6,986.8 ± 1,091.5 ^{ab}	1,124.1 ± 193.4	1,394.8 ± 347.1 ^{ab}	2,969.3 ± 402.4 ^{ab}	1,124.1 ± 193.4
High visual obstruction (%; 0.5–1.0 m)	22.1 ± 7.2 ^{ab}	46.2 ± 4.7 ^{ab}	17.8 ± 0.9	15.2 ± 1.6 ^{ab}	29.8 ± 1.8 ^{ab}	17.8 ± 0.9
Distance to complete visual obstruction (m)	47.4 ± 7.5	28.2 ± 4.9 ^b	38.8 ± 0.9	52.2 ± 1.9 ^{ab}	36.6 ± 2.3 ^{ab}	38.8 ± 0.9

^a Ho: $\frac{\text{Feeding} + \text{bedding}}{2} = \text{randoms}$.

^b Ho: Feeding = bedding.

TABLE 3.—Hiding cover variables collected at white-tailed deer feeding, bedding, and random locations on summer range in the central Black Hills, South Dakota and Wyoming, 1993–1996. Orthogonal contrasts were conducted to compare differences between feeding, bedding, and random locations^a and differences between feeding and bedding locations^b within sex and season.

	Summer locations of males			Summer locations of females		
	Feeding	Bedding	Feeding	Bedding	Feeding	Bedding
	$\bar{X} \pm SE$ <i>n</i> = 6	$\bar{X} \pm SE$ <i>n</i> = 21	$\bar{X} \pm SE$ <i>n</i> = 148	$\bar{X} \pm SE$ <i>n</i> = 266	$\bar{X} \pm SE$ <i>n</i> = 559	$\bar{X} \pm SE$ <i>n</i> = 559
Basal area (m ² /ha)	13.4 ± 3.6	15.1 ± 1.9	12.8 ± 0.7 ^{ab}	15.6 ± 0.6 ^{ab}	11.6 ± 0.4	11.6 ± 0.4
Average DBH (cm)	8.6 ± 2.0	9.3 ± 1.1	10.0 ± 0.4 ^{ab}	8.9 ± 0.3 ^{ab}	8.6 ± 0.2	8.6 ± 0.2
Density of tall shrubs and saplings (stems/ha)	3,250.0 ± 1,410.3 ^a	2,928.6 ± 753.8 ^a	2,082.8 ± 358.5 ^{ab}	3,429.5 ± 267.4 ^{ab}	1,022.4 ± 146.1	1,022.4 ± 146.1
High visual obstruction (%; 0.5–1.0 m)	32.8 ± 10.8 ^a	53.6 ± 5.8 ^a	36.8 ± 2.2 ^{ab}	49.5 ± 1.6 ^{ab}	26.3 ± 1.1	26.3 ± 1.1
Distance to complete visual obstruction (m)	32.7 ± 15.3	24.0 ± 8.2	27.0 ± 2.5 ^a	23.6 ± 1.9 ^a	39.2 ± 1.3	39.2 ± 1.3

^a Ho: $\frac{\text{Feeding} + \text{bedding}}{2} = \text{randoms}$.

^b Ho: Feeding = bedding.

9.0, *d.f.* = 1, 970, *P* = 0.003), density of tall shrubs and saplings (*F* = 9.1, *d.f.* = 1, 970, *P* = 0.003), and percentage high visual obstruction (*F* = 21.5, *d.f.* = 1, 970, *P* ≤ 0.001) were greater at bedding than at feeding sites, while average DBH (*F* = 5.5, *d.f.* = 1, 970, *P* = 0.020) was greater at feeding than at bedding sites (Table 3).

On winter range, density of tall shrubs and saplings (*F* = 8.4, *d.f.* = 1, 552, *P* = 0.004) and percentage high visual obstruction (*F* = 13.9, *d.f.* = 1, 552, *P* ≤ 0.001) were greater for males bedding than at feeding or random locations (Table 2). Similarly, density of tall shrubs and saplings (*F* = 8.4, *d.f.* = 1, 552, *P* = 0.004), percentage visual obstruction (0.5–1.0 m; *F* = 7.8, *d.f.* = 1, 552, *P* = 0.005), and distance to complete visual obstruction (*F* = 4.6, *d.f.* = 1, 552, *P* = 0.033) for males differed between bedding and feeding locations; density of tall shrubs and saplings and percentage visual obstruction were greater at bedding than at feeding sites, while distance to total visual obstruction was greater at feeding than at bedding locations (Table 2). Conversely, on summer range for male white-tailed deer, density of tall shrubs and saplings (*F* = 6.5, *d.f.* = 1, 583, *P* ≤ 0.011) and percentage visual obstruction (0.5–1.0 m; *F* = 7.4, *d.f.* = 1, 583, *P* = 0.007) differed between feeding, bedding, and random locations; density of tall shrubs and saplings were greater at feeding than at bedding and random sites, while percentage visual obstruction was greater at bedding than at feeding and random locations (Table 3).

A total of 78.5% of the variation in basal area, average DBH, density of tall shrubs and saplings, high visual obstruction, and distance to total visual obstruction was explained by the first 3 principal components. Principal component 1, interpreted as hiding cover, was a contrast between high visual obstruction and distance to total visual obstruction [*Y*₁ = 0.84(high visual obstruction) – 0.83(distance to total visual obstruction) + 0.58(density of tall shrubs and saplings) + 0.05(average DBH) +

0.12(basal area)]; these variables (measured as high visual obstruction, density of tall shrubs and saplings, and distance to total visual obstruction) represent the ability of deer to hide from predators. Principal component 2, interpreted as thermal cover, was characterized primarily by average DBH [$Y_2 = 0.14(\text{high visual obstruction}) + 0.22(\text{distance to total visual obstruction}) + 0.49(\text{density of tall shrubs and saplings}) - 0.93(\text{average DBH}) + 0.03(\text{basal area})$]; tree size (measured as average DBH) intercepts wind and influences convective heat transfer (Moen 1968). Principal component 3, interpreted as radiation cover, was characterized primarily by basal area [$Y_3 = -0.12(\text{high visual obstruction}) + 0.13(\text{distance to total visual obstruction}) + 0.27(\text{density of tall shrubs and saplings}) + 0.07(\text{average DBH}) - 0.96(\text{basal area})$]; radiant heat loss (measured as basal area) is related to overstory canopy cover. Thus, principal component scores were interpreted as forming axes of visual (hiding), wind (thermal), and vertical (radiation) cover.

Principal component scores did not differ for activity ($F = 0.973$, $d.f. = 3$, 680, $P = 0.405$). However, differences in principal component scores were apparent for sex within winter ($F = 2.470$, $d.f. = 3$, 335, $P = 0.062$) with separation along principal components 1 (hiding: females, $n = 304$, $\bar{X} = -0.48 \pm 0.06$; males, $n = 35$, $\bar{X} = -0.16 \pm 0.16$) and 3 (radiation: females, $n = 304$, $\bar{X} = 0.03 \pm 0.06$; males, $n = 35$, $\bar{X} = -0.36 \pm 0.18$) and for summer ($F = 3.052$, $d.f. = 3$, 506, $P = 0.028$) with separation along principal components 1 (hiding: females, $n = 477$, $\bar{X} = 0.32 \pm 0.41$; males, $n = 33$, $\bar{X} = -0.08 \pm 0.16$) and 2 (thermal: females, $n = 477$, $\bar{X} = -0.08 \pm 0.05$; males, $n = 33$, $\bar{X} = -0.46 \pm 0.17$).

DISCUSSION

Typically, sexual segregation is defined as a differential use or partitioning of available resources between sexes outside of the breeding season (Geist and Petocz 1977; Main and Coblentz 1990; Main et al. 1996;

McCullough 1979). The resulting resource partitioning is thought to lessen competition between the sexes and enhance reproductive success (Bleich 1993; Bleich et al. 1997; Bowyer 1984; Main et al. 1996). Essentially, sexual segregation is resource partitioning in association with spatial or geographic separation (Bleich et al. 1997; Bowyer 1984; Kie and Bowyer 1999; Main et al. 1996). Resource partitioning, or differential use of habitat between the sexes, however, can occur without spatial separation (Kie and Bowyer 1999). In our study, we do not present such spatial data in support of sexual segregation. Habitat characteristics can be viewed as resources that can be partitioned; however, when distributed as discrete patches of habitat, they could indeed lead to sexual segregation in ungulates (Kie and Bowyer 1999; Main et al. 1996; McCullough et al. 1989).

Although numerous hypotheses exist to explain the presence of resource partitioning and sexual segregation in sexually dimorphic ungulates (Barboza and Bowyer 2000; Bleich 1993; Bleich et al. 1997; Geist and Petocz 1977; Main and Coblentz 1990, 1996; Main et al. 1996; Miquelle et al. 1992; Post et al. 2001), there is only substantial support for an accredited few. Recently, these hypotheses have been grouped into 3, although not mutually exclusive, categories consisting of the RSH, the sexual dimorphism-body size hypothesis, and the social-factors hypothesis (Main et al. 1996; Miquelle et al. 1992; Ruckstuhl and Neuhaus 2000). Other hypotheses that have been proposed to explain segregation include foraging behavior (Ruckstuhl 1998), gut capacity (Barboza and Bowyer 2000; Jenks et al. 1994), and other morphological differences (Post et al. 2001; Ruckstuhl 1998). Moreover, the PAH (Bleich 1993; Bleich et al. 1997; Geist 1982) has recently been incorporated into the RSH (Main et al. 1996).

The RSH predicts that males and females use habitats differently to increase reproductive fitness (Bleich 1993; Bleich et al.

1997; Geist and Petocz 1977; Main and Coblenz 1990; Main et al. 1996; Miquelle et al. 1992; Weckerly 1993). Specifically, males should exploit high-quality habitats and avoid areas that are less productive. Because females reduce quality of habitats for males, males should avoid habitats used by females and young (Main et al. 1996). Geist and Petocz (1977) proposed that, by remaining near the female and young, males could reduce growth and development of their offspring by depriving them of resources, impairing the physiological condition of females for the next season, and risking the underdevelopment and mortality of future offspring. The RSH has been a primary explanation for resource partitioning and sexual segregation in sexually dimorphic ungulates (Bleich 1993; Bleich et al. 1997; Ginnett and Demment 1999; Kie and Bowyer 1999; Main and Coblenz 1990; Main et al. 1996; Miquelle et al. 1992). However, some investigators have reported that, when segregated, females occupy areas with higher quality forage than males (Beier 1987; Beier and McCullough 1990; Bowyer 1984; Charles et al. 1977; Clutton-Brock et al. 1987; Post et al. 2001; Shank 1985; Staines et al. 1982; Watson and Staines 1978).

Predation has been proposed to influence habitat selection (Berger 1991; Bowyer et al. 1999; Kie 1999; Kohlmann et al. 1996; Lima and Dill 1990; Rachlow and Bowyer 1998) and thus, sexual segregation. The PAH suggests that spatial separation of the sexes occurs because mature males are less susceptible to predators than the smaller females and young (Bleich 1993; Bleich et al. 1997; Geist 1982). Furthermore, the PAH is based on the fact that mature males, by way of their greater freedom of movement, differentially use high-predation areas to maximize nutrient intake (Bleich 1993; Bleich et al. 1997; Festa-Bianchet 1988; Geist 1982; King and Smith 1980; Main and Coblenz 1990, 1996; McCullough et al. 1989). Females, however, are thought to avoid habitats that provide superior forag-

ing opportunities in preference to those that provide security to raise offspring (Main and Coblenz 1990). Thus, by using habitats differently, males are able to maximize nutrient intake (Festa-Bianchet 1988; Geist 1982; King and Smith 1980; Kohlmann et al. 1996; Main and Coblenz 1990; McCullough et al. 1989), while females and young minimize risk of predation (Frid 1994; Kohlmann et al. 1996; Ober 1931). In support of this hypothesis, Bleich et al. (1997) concluded that male mountain sheep (*Ovis canadensis nelsoni*) obtained a higher quality diet from habitats with high predator densities compared with females; females were located in habitats with steeper, more open slopes and relatively low predator densities. Furthermore, Post et al. (2001) provided evidence that diet choice of female bison (*Bison bison*) was not constrained by the need to protect offspring.

Main and Coblenz (1996) reported that female mule deer selected areas that contained greater amounts of hiding cover than males. Similarly, roe deer (*Capreolus capreolus*) bedded in areas that provided abundant cover, whereas they primarily fed in areas with little or no cover (Mysterud and Ostbye 1995). The results of our study indicate that, on winter range, female white-tailed deer tended to select habitats that contained lower amounts of hiding cover than habitats selected by males, and females generally bedded on winter range in areas that were characterized by greater hiding cover than feeding and random sites. Moreover, the high sapling density observed at winter bed sites indicated that these microhabitats provided greater cover than sites with lower sapling densities.

In early spring, male and female deer migrate from low-elevation winter ranges to high-elevation summer ranges, where there is significantly more hiding cover (DePerno 1998; DePerno et al. 2002; Klaver 2001). At this time, females seek isolation in areas where hiding cover is abundant (King and Smith 1980). Fox and Krausman (1994) suggested that condition and type of cover

used for fawning may influence fawn survival and that activity in areas of sparse vegetation would attract predators. Hiding cover is important to neonates, which are more susceptible to predation than adults and therefore are more dependent on cover for escape and concealment (Loft et al. 1987). In this study, females bedded in locations on summer range that contained greater amounts of hiding cover than feeding locations. They also selected cover characteristics (bedding and feeding sites) at levels greater than at random sites. Overall, females selected sites with high amounts of deciduous canopy cover, slash, visual obstruction, and lower amounts of shrub and forb cover (DePerno 1998; DePerno et al. 2002; Klaver 2001). However, when feeding and bedding sites were combined, no discernible difference was apparent for cover characteristics selected by males and females (Table 1). These results are in contrast with the RSH, which states that males and females will use habitats differently to increase reproductive fitness (Geist and Petocz 1977).

Hiding, thermal, and radiation cover have been documented as important components of habitat selection by white-tailed deer, particularly in winter (Moen 1968; Parker and Gillingham 1990). Hiding cover is important for avoidance of predators and has been linked to fawn survival (DePerno et al. 2000; Hamlin et al. 1984; King and Smith 1980). Compared with open habitats, forested habitats are often cooler in summer and variation in temperature and wind speeds are reduced in winter (Bunnell et al. 1986; Parker and Gillingham 1990). Adequate thermal and radiation cover allow animals to maintain body core temperatures and thus minimize thermoregulatory costs (Hanley et al. 1989). Models that incorporate animal energetics represent a more consistent approach to understanding behavior (Wilson 1999).

In winter, males and females were separated along components 1 (hiding cover) and 3 (radiation cover). When principal

component means were compared, males had higher scores for hiding cover (component 1), while females had higher scores for radiation cover (component 3). Male and female white-tailed deer are dimorphic, with females weighing 20–40% less than males (Smith 1991). Larger animals with lower surface-to-volume ratios and higher absolute metabolism are able to endure longer exposures to harsh environments than smaller animals that respond more quickly to environmental changes and, consequently, may benefit from habitats with high cover characteristics (Moen 1978; Parker and Gillingham 1990). As air temperature declines, heat loss from the animal's surface increases due to convection (Moen 1968). Therefore, females in this study experienced physiological benefits by occupying habitats with characteristics of high radiation cover. Furthermore, solar radiation may increase the ability of an animal to withstand cold air temperatures and may potentially decrease metabolic rates (Grojean et al. 1980). In summer, males and females were separated along components 1 (hiding cover) and 2 (thermal cover). When principal component means were compared, females had higher scores for hiding cover (component 1) and thermal cover (component 2) than males. These results indicate that hiding cover was of greater importance to female than to male white-tailed deer on summer range.

Evaluation of the data in three-dimensional space indicated that, on winter range, females were primarily concerned with body maintenance (i.e., radiation cover), whereas it appears that hiding cover was more important to males than females on winter range. Because females and their young are more susceptible to predation than males, for the PAH to be accepted, hiding cover would need to be more important to female than to male white-tailed deer. Because this was not the case, evaluation of the winter range data in both the univariate and multivariate analyses indicated that males and females were not par-

TABLE 4.—Results of seasonal evaluation of the predator-avoidance hypothesis and reproductive-strategy hypothesis for white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

	Predator-avoidance hypothesis	Reproductive-strategy hypothesis
Winter	Reject Males > hiding cover Females > radiation cover	Fail to reject Different univariate results
Summer	Fail to reject Females > hiding cover Females > thermal cover	Reject Similar univariate results

tioning hiding cover to avoid predators. These results support rejection of the PAH on winter range (Table 4).

Bowyer (1984) postulated that sexual segregation in southern mule deer was not attributable to food habitats or habitat selection but likely occurred as a result of water requirements; increased water needs of lactation drove segregation. Conversely, our results indicate that selection of preferred habitats is likely the driving force behind the observed resource partitioning on summer range in the central Black Hills. Evaluation of the data in three-dimensional space indicated that females were more concerned with predator avoidance (i.e., hiding cover) than male white-tailed deer but were no closer to water sources than males. If females were responding to predators by fawning in areas with greater hiding cover, then we hypothesize that, in the absence of predators, females would select habitats similarly to males. Thus, we were unable to reject the PAH on summer range in the central Black Hills. However, these results, coupled with similar univariate results between the sexes (Table 1), provide support for rejecting the RSH on summer range in the central Black Hills (Table 4).

Activity levels of radiocollared white-tailed deer further support the above conclusions. Males were bedded at 64% of locations on winter range compared with 48% for females. During winter months, increased time spent bedding by males in thick cover likely conserves energy. Fe-

males were feeding a greater percentage of the time on both summer (37%) and winter ranges (52%) compared with males (i.e., summer, 14%; winter, 36%). Increased time spent feeding by females may be a function of their requirement for greater quantities of forage during both summer lactation (Jenks et al. 1994) and possibly winter gestation. Conversely, males do not have extreme energy demands during these periods and can spend more time conserving energy. Thus, habitat use by females may be more a function of vegetative characteristics that involve forage and hiding cover, whereas habitat use of males may be more a function of behavior and social factors (Ordway and Krausman 1986).

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