Selection of Sites for Winter Night Beds by White-tailed Deer in a Hemlock-Northern Hardwood Forest[1]

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ABSTRACT: Environmental factors influencing selection of sites for winter night beds by white-tailed deer (*Odocoileus virginianus*) were evaluated in an eastern hemlock (*Tsuga canadensis*)—northern hardwood forest in western Maryland. Sixty-two microhabitat variables were sampled at 140 bed sites to characterize vegetation structure and cover. Microhabitat variables at bed sites were compared to 100 random sites to determine factors involved in site selection. Principal components analysis (PCA) of the random sites using variables important in night-bed selection resulted in four PCs that defined a four-dimensional PC space upon which the microhabitats of the 140 bed sites were plotted. Night beds were characterized by more coniferous cover directly above the bed, a greater frequency of eastern hemlock trees N and W of the bed, an open southeastern exposure, a low minimum distance to the nearest tree and a high spatial heterogeneity of trees.

Introduction

The behavior of white-tailed deer (*Odocoileus virginianus*) with respect to winter weather conditions has been considered by many investigators (Cook and Hamilton, 1942; Severinghaus, 1947; Telfer, 1967, 1970, 1978; Ozoga, 1968; Verme, 1968; Verme and Ozoga, 1971; Ozoga and Gysel, 1972; Kucera, 1976). In general, these studies have indicated that deer seek dense cover for energy conservation and protection from the adverse conditions of winter. A number of authors have noted that wintering areas of deer tend to occur on level bottomland with a high proportion of conifers (Webb, 1948; Verme, 1965, 1968; Ozoga, 1968; Ozoga and Gysel, 1972; Hout, 1974; Moen, 1976; Euler and Thurston, 1980; Gates and Harman, 1980). These coniferous bottomlands are reportedly favored by deer because of shallower snow depths, better quality of support by the snow, higher average temperature, narrower range of temperature fluctuations and decreased velocity of wind.

Particular stands of conifers not only offer a most effective buffer against loss of body heat by convection and radiation (Moen, 1968a; Ozoga, 1968), but also provide a more stable environment where deer may select optimal microhabitats for energy conservation. Bed-site selection is an easily recognizable behavioral response to those microhabitats that offer optimal conditions for survival during severe winter weather (Robinson, 1960; Euler and Thurston, 1980; Gates and Harman, 1980; Armstrong *et al.*, 1983). Although Armstrong *et al.* (1983) compared the habitat at night and day beds in central Ontario, no one has investigated the microhabitat factors associated with selection of sites used for night beds from among the available sites within a wintering area. The objective of this study was to determine which microhabitat factors were most associated with sites chosen for night beds by white-tailed deer in an eastern hemlock (*Tsuga canadensis*)—northern hardwood wintering area.

Study Area

The study area, located on the Allegheny Plateau in northeastern Garrett Co., Maryland, forms a portion of the watershed for the City of Frostburg, Md. (Gates and Harman, 1980). The deer wintering area borders Blandy Run Creek, which flows

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from the E into the Frostburg reservoir. The topography is formed of rolling tableland with 10-35% slopes and nearly level, alluvial bottomland along Blandy Run. The floodplain is composed of moderately deep, well-drained, very stony soils formed in mixed, variable material (Stone and Matthews, 1974). Elevations range from 716 m at the reservoir to 823 m above sea level on bordering ridge crests.

Three habitat types are found within the deer wintering area (Gates and Harman, 1980). The overstory and understory species composition of the NE-facing slope is dominated by eastern hemlock and sugar maple (*Acer saccharum*), making up 82.9% of all individual species and 84.8% of the basal area. On the SW-facing slope, sugar maple comprises 37.4% of all individual species and 55.0% of the basal area in these two strata. Red oak (*Quercus rubra*) accounts for an additional 22.1% of the basal area. Eastern hemlock, red maple (*A. rubrum*) and yellow birch (*Betula lutea*) dominate in the bottomland, comprising 33.8%, 17.3% and 11.5% of all individual species, respectively. These three species account for 61.9% of the basal area.

The Allegheny Plateau has a humid continental climate with general atmospheric flow from W-E. Annual precipitation averages more than 114 cm. The coldest, most severe weather occurs in January and February with prevailing winds from the W-NW and average annual snowfalls of 180 cm (Stone and Matthews, 1974).

MATERIALS AND METHODS

Field procedures. — Nine transects, 35 x 700 m, were established within the study area oriented with their long axis across the deer wintering area and perpendicular to Blandy Run. Each transect was divided into 20, 35 x 35 m sample plots for ease in locating bed sites. The area covered by all nine transects totaled 22.05 ha. Each transect was surveyed for bed sites at sunrise, generally one to three times per week, from January through mid-March 1981 and January 1982, as long as snow remained on the ground. In late afternoon of the day before a bed-site survey, the sample plots were cleared of old night and day beds by brushing snow into the bed. Maximum-minimum thermometers located at three permanent weather stations on the SW-facing slope, bottomland and NE-facing slope were also set. Before conducting a bed-site survey on the next morning, overnight maximum-minimum temperatures and five random snow-depth measurements were recorded at the three weather stations.

After recording the weather conditions, fresh beds formed during the previous night were located and marked with aluminum tags for later microhabitat analysis. Microhabitat measurements were taken in late March and April before leaf-out in order to quantify the composition and structure of winter vegetative cover. Sixty-two microhabitat variables were sampled at 108 night-bed and 100 random sites in 1981 (Appendix). Thirty-two additional night-bed sites were sampled in 1982. Random sample points were located within the eastern hemlock-red maple-yellow birch cover type using a stratified-random sampling design.

Statistical analysis. — Both parametric and nonparametric statistical tests were used to analyze the data. Values skewed or kurtic were transformed using either logarithmic, $Z = \log_{10}(X + 1)$, or square root, $Z = \sqrt{X}$, transformations. Data were analyzed with ANOVA to test for differences between sites used for night beds and random sites. Bartlett's test was used to test for homogeneity of variance (Sokal and Rohlf, 1969). Densiometer values could not be normalized by data transformation (Lemmon, 1956). Therefore, these variables were analyzed using a nonparametric statistical test, the Mann-Whitney U test (Siegel, 1956). Chi-square (X^2) tests corrected for continuity (Siegel, 1956) were used to test whether or not the occurrence of different tree species in each of the four quadrants (N, E, S, W) at night-bed sites differed from random sites.

Principal components analysis (PCA) was used to reduce the dimensionality of the microhabitat data set (Dixon, 1977; Neff and Marcus, 1980). Due to the problems associated with using a large number of variables in a multivariate analysis (Green, 1979), the number of variables included in PCA was reduced to 11 based upon observed parametric differences ($P<0.10$) between sites used for night beds and random sites. The PCA was conducted using only the random sites in order to delineate the available microhabitat space within which night-bed microhabitats were subsequently plotted. This two-dimensional ordination space formed by PC-I and PC-II can be viewed as a rectangle with outer boundaries defined by lines perpendicular to the minimum and maximum values of the random sites along each PC. Bed and random site group centroids for each PC were plotted to facilitate interpretation of the ordination patterns. Median values of the random sites were also plotted in the two-dimensional ordination space. Bed sites were compared against an expected equal frequency distribution in each quadrant formed by the two intersecting random-site medians using a one-sample chi-square (X^2) test (Siegel, 1956). The frequency of all PC scores occurring along each PC were also determined to clarify the distribution of bed sites within the available microhabitat space. The statistical theory behind PCA is described in Gauch (1982).

RESULTS

Because we did not observe behavioral differences in night-bed selection by deer from one year to the next and because January environmental conditions were similar in 1981 and 1982, the five surveys conducted in January 1982 were added to the 20 completed in 1981. The number of night beds found on the area per visit ranged from 0-28 ($\bar{x} = 5.6 \pm 1.5$ SE). Overnight minimum temperatures were significantly colder ($t = 2.97$, $df = 21$, $P<0.01$) during the visits when night beds were found ($\bar{x} = -17.3$ C $\pm$ 1.9 SE, $n = 14$) compared to those when night beds were absent ($\bar{x} = -8.9$ C $\pm$ 1.9 SE, $n = 9$). Overnight minimum temperatures during January and February ranged from -26.0 C to -3.5 C ($\bar{x} = -16.6$ C $\pm$ 1.5 SE, $n = 18$) in the bottomland wintering area. Overnight minimum temperatures in March were 8.9-19.0 C warmer. Average snow depths during the study ranged from 11.2 cm on the bottomland to 21.7 cm on the NE-facing slope, with the SE-facing slope being intermediate (18.1 cm). The NE-facing slope also recorded the deepest snow depth during the study period, 42.0 cm.

Based on densiometer measurements, there was significantly ($P<0.01$) more cover (MAXDENS, MINDENS, MEANDENS) immediately above the night-bed sites than above the random sites (Table 1). The ANOVA of microhabitat variables at 140 bed sites compared with 100 random sites also revealed differences between the two groups for eight of 62 microhabitat variables. Bed sites had significantly ($P<0.05$) lower cover to the SE from ground level to 1 and 1.5 m at distances of 5 [(I, II)SE5] and 10 m [(I–III)SE10], respectively, than did random sites (Fig. 1). However, bed sites had more cover to the SE 5 m from the bed at a height of 2.5 m (VSE5) than did random sites. The only other significant differences occurred in the spatial arrangement of trees around the bed site (Table 1). Minimum distance (MINDIST) to the nearest tree in each of four quadrants around the bed site was significantly less ($P<0.01$) than at random sites. The spatial heterogeneity (HETINDEX) of trees was also significantly greater ($P<0.01$) at night-bed than at random sites.

Chi-square (X^2) tests for randomness of occurrence of species of trees around bed sites indicated that eastern hemlock was present more often than expected ($P<0.05$) in the N and W quadrants (Table 2). Red maple was present less than expected ($P<0.01$) in the N quadrant. Black cherry was also present less than expected ($P<0.05$) in the S quadrant.

Four PCs accounting for 72.5% of the total variance of the random-site microhabitats were extracted from an 11 variable correlation matrix (Table 3). Principal component I explained 30.8% of the variance in the data matrix. Cover toward the SE from ground level to 1.5 m recorded at a distance of 10 m [(I-III)SE10] from the random site was most positively correlated with PC-I. Night beds tended to have lower ($X^2 = 11.43$, $df = 1$, $P<0.001$) values on this PC than did random sites (Fig. 2). Principal component II accounted for an additional 20.7% of the variance in the data matrix. This component is primarily a measure of microspatial variability of tree distribution. MINDIST and MEANDIST were positively correlated with PC-II, whereas HETINDEX was negatively correlated. Night beds generally had lower ($X^2 = 29.26$, df = 1, $P<0.001$) values on PC-II (Fig. 2). Cover values IISE5 and ISE5 were positively correlated with PC-III, which accounted for 10.9% of the data variance. Night-bed sites showed very little separation along this PC. Positively correlated with PC-IV was variable VNW5. Although PC-IV accounted for 10.1% of the data variance in addition to that already explained, assessment of two-dimensional ordinations involving this PC also contributed little additional information. In spite of the fact that deer showed wide variation in microhabitat selection along the PCs (Fig. 2), they did tend to select bed sites within certain portions of the available microhabitat space (Table 4).

DISCUSSION

Night beds were more abundant under certain environmental conditions in the bottomland wintering area. Based on our observations of snow trails and tracks, we discovered that deer entered the dense hemlock cover during severe weather conditions (*i.e.*, very low temperatures coupled with gusty, high winds). Because snow depths rarely exceeded the critical 40-cm depth reported to impair deer movement considerably (Kelsall, 1969), deer left the hemlock cover once the weather moderated, ap-

TABLE 1.—Means and 95% confidence intervals of microhabitat variables sampled at bed and random sites within the deer wintering area. Except where indicated, probabilities were based upon one-way ANOVA

Variable code (*see* Appendix)	Bed site (N = 140)		Random site (N = 100)	
	$\bar{x}$	95% CI	$\bar{X}$	95% CI
DECIDBA (m^2/ha)	18.1	17.0- 19.0	18.4	17.4- 19.7
CONIFBA (m^2/ha)	11.9	11.0- 12.6	10.8	9.6- 11.9
TOTALBA (m^2/ha)	29.8	28.7- 31.2	29.4	28.0- 30.5
MAXDENS (%)[1]	95.5	94.0- 96.8	84.9**	80.8- 89.1
MINDENS (%)[1]	92.8	91.3- 94.3	82.8**	78.7- 86.9
MEANDENS (%)[1]	94.1	92.7- 95.6	84.0**	79.8- 88.1
MAXDIST (m)	4.6	4.4- 4.8	4.4	4.2- 4.7
MINDIST (m)	1.3	1.2- 1.4	1.7**	1.5- 1.9
MEANDIST (m)	2.9	2.7- 3.0	3.1†	2.9- 3.2
HETINDEX (%)	52.1	48.7- 55.4	42.5**	38.9- 46.1
IBEAR (°)[2]	356.0	351.5- 0.6	0.1	354.9- 5.3
IDIST (m)	2.4	2.1- 2.6	2.7	2.4- 3.0
IDBH (cm)[2]	19.5	17.6- 21.6	17.3	15.5- 19.3
IIBEAR (°)	90.7	86.4- 94.9	93.6	88.9- 98.4
IIDIST (m)	3.0	2.8- 3.3	3.2	2.9- 3.5
IIDBH (cm)[2]	18.2	16.5- 20.0	17.0	15.3- 18.8
IIIBEAR (°)	179.6	175.2-184.1	181.4	176.3-186.5
IIIDIST (m)	3.0	2.8- 3.3	3.1	2.8- 3.3
IIIDBH (cm)[2]	16.7	15.3- 18.2	17.5	16.0- 19.2
IVBEAR (°)	271.0	266.6-275.4	275.6	270.9-280.3
IVDIST (m)	2.7	2.4- 3.0	2.9	2.6- 3.2
IVDBH (cm)[2]	17.3	15.9- 18.9	17.7	16.0- 19.5

[1]Differences analyzed with Mann-Whitney U test

[2]Variables were transformed using the formula, $Z = \log_{10}(X + 1)$. Means and 95% confidence intervals were transformed back into linear scale by calculating their antilogarithms

† $P<0.10$

* $P<0.05$

** $P<0.01$

parently for better browsing areas elsewhere. In fact, no beds were found during five visits in March, a time of more moderate weather conditions. Many studies indicate that reduction of wind is one of the most important benefits of coniferous cover in winter and that increasing wind chill directly influences the shelter-seeking response exhibited by white-tailed deer (Robinson, 1960; Verme, 1965, 1968; Verme and Ozoga, 1971; Ozoga and Gysel, 1972; Gates and Harman, 1980). Indeed, Euler and Thurston (1980) noted that wind flow at bedding sites located within hemlock cover was 64% less than over control sites located outside such cover.

Although many suitable sites for night-bedding appeared to be available to deer within the eastern hemlock-red maple-yellow birch habitat type of the bottomland, deer did favor bed sites with specific microhabitat characteristics: (1) an open southeastern exposure; (2) hemlock trees to the W and N; (3) a high spatial

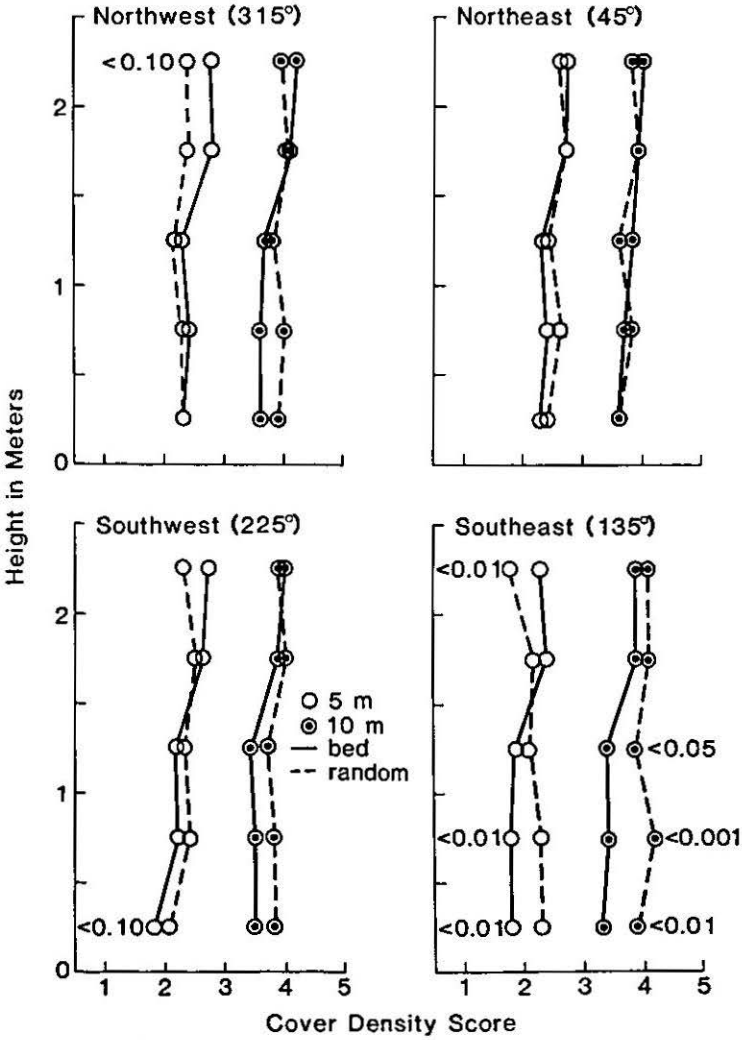

Fig. 1.—Cover density scores recorded at two distances, 5 and 10 m, and four compass bearings around bed (N = 140) and random (N = 100) sites

TABLE 2.—Results of chi-square test for randomness of nearest tree species occurring in each of four quadrants at bed (N = 140) and random (N = 100) sites

	North (>315-45°)		East (>45-135°)		South (>135-225°)		West (>225-315°)	
Species	Bed	Random	Bed	Random	Bed	Random	Bed	Random
Tsuga canadensis	56.4	34.0**	43.6	38.0	45.7	34.0	52.9	37.0*
Acer rubrum	5.7	21.0**	13.6	10.0	12.1	20.0	10.0	18.0
A. saccharum	3.6	10.0	6.4	11.0	8.6	6.0	4.3	10.0
Fagus grandifolia	9.3	8.0	10.7	12.0	10.7	8.0	9.3	14.0
Prunus serotina	8.6	11.0	8.6	11.0	4.3	12.0*	5.7	6.0
Betula lutea	8.6	11.0	10.7	10.0	10.0	14.0	10.7	11.0
B. lenta[1]	0.7	1.0	0.7	1.0	0.7	2.0	0.0	1.0
Quercus alba[1]	0.0	0.0	0.0	0.0	1.4	1.0	0.0	0.0
Q. rubra[1]	3.6	1.0	0.7	2.0	0.7	1.0	0.7	1.0
Q. prinus[1]	0.0	0.0	1.4	0.0	1.4	0.0	0.0	0.0
Ostrya virginiana[1]	0.7	0.0	0.7	1.0	0.7	0.0	1.4	1.0
Carpinus caroliniana[1]	0.0	1.0	0.7	4.0	0.0	0.0	0.0	1.0
Snag[1]	2.9	2.0	2.1	0.0	3.6	2.0	5.0	0.0

[1]Inadequate sample size
* $P<0.05$
**$P<0.01$

TABLE 3.—Reordered factor pattern showing loadings (correlations) of the variables with the principal components based upon orthogonal rotation. Loadings greater than 0.700 are underlined

	Principal component				
Variable code (*see* Appendix)	I	II	III	IV	Communality
IISE10	0.898	0.008	0.208	0.097	0.859
IIISE10	0.838	0.008	0.277	−0.015	0.779
ISE10	0.810	−0.082	0.240	0.000	0.721
MINDIST	−0.037	0.942	0.051	−0.095	0.900
HETINDEX	−0.074	−0.813	0.087	−0.092	0.683
MEANDIST	−0.117	0.774	0.126	−0.131	0.645
IISE5	0.225	−0.041	0.877	0.011	0.822
ISE5	0.250	0.005	0.820	−0.069	0.739
VSE5[1]	0.260	0.213	0.568	0.309	0.531
VNW5	−0.128	−0.047	0.192	0.853	0.784
ISW5[1]	0.372	−0.127	−0.239	0.543	0.507
Eigenvalue	3.384	2.284	1.201	1.103	7.972
Relative percentage of total variance accounted for by the principal components	30.8	20.7	10.9	10.1	
Cumulative percentage of total variance accounted for by the principal components	30.8	51.5	62.4	72.5	

[1]Variables were transformed using the formula, $Z = \log_{10}(X + 1)$

heterogeneity of tree distribution; (4) near a tree; and (5) dense cover immediately above the bed site. An open southeastern exposure may allow for greater influx of morning solar radiation at the bed site (Robinson, 1960), provide for an open visual field or serve as an escape route. An open visual field to the SE is critically important

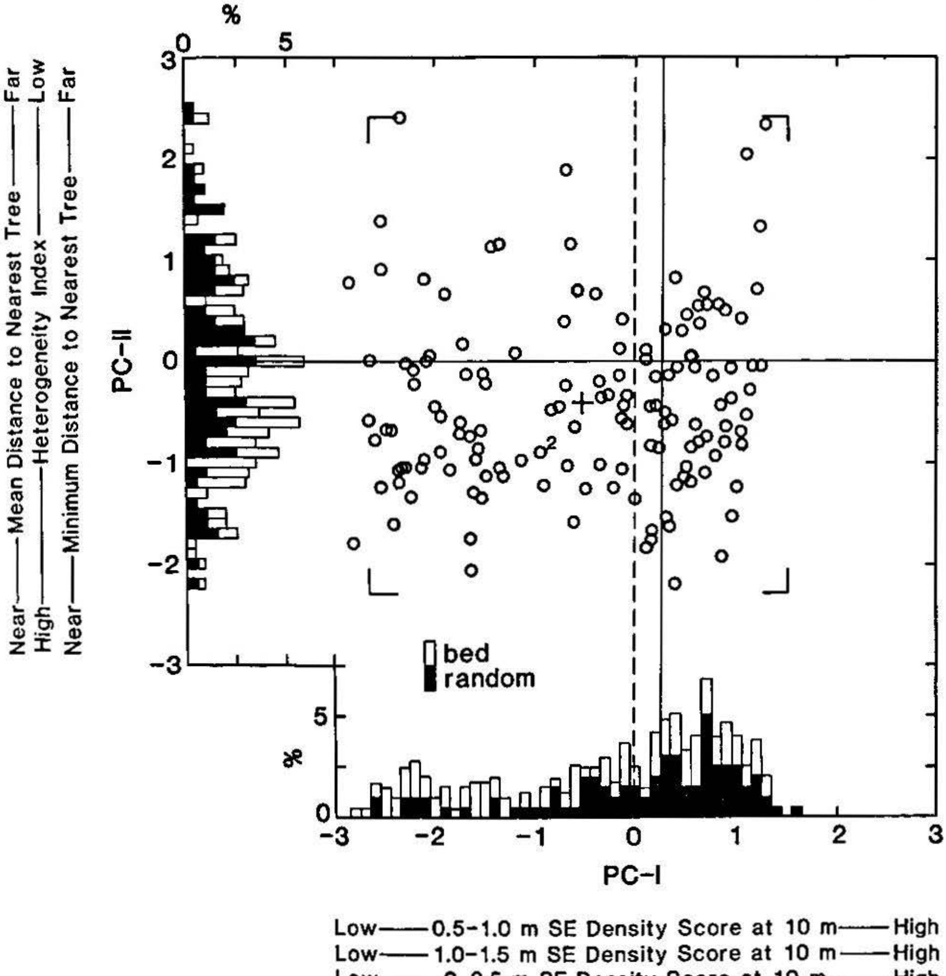

Fig. 2.—Two-dimensional ordination of microhabitats of 140 bed sites (circles) within the principal component (PC) space of the available microhabitats enclosed by four corners and defined by PC-I and II. The location of the means and medians of the PC space representing the available microhabitats are indicated by dashed and solid lines, respectively

TABLE 4.—One-sample chi-square tests of the number of night beds present in each of four quadrants formed by the two medians of the random sample in PC space (Fig. 2). Quadrants are numbered sequentially in a clockwise fashion beginning with the upper right hand quadrant

PC-axes		Quadrant					
X	Y	I	II	III	IV	X^2	P
I	II	16	34	68	22	46.29	<0.001

when winds carrying scent stimuli are from the W-NW. Since deer reduce radiant and convective heat loss most effectively by seeking heavy coniferous cover (Moen, 1968a,b; Verme, 1968), deer should select effective thermal cover in the direction of the prevailing winds (Moen, 1973), which are W-NW in the Allegheny Plateau region (Stone and Matthews, 1974). Although there were no significant differences in cover density to the NW at 5 and 10 m from night-bed or random sites, deer did selectively choose microhabitats with more eastern hemlock trees in the W and N night-bed quadrants (Armstrong *et al.*, 1983). Possibly cover density closer than 5 m from the bed site was more important. Additionally, deer chose microhabitats with more microspatial variation in tree dispersion around the night-bed site than was present at the random sites, *i.e.*, the available microhabitats. Perhaps this was because deer also selected bed sites near trees (Armstrong *et al.*, 1983), thereby increasing the spatial heterogeneity index recorded at the bed site. Nonetheless, such spatial variation in tree dispersion can result in microspatial differences in climate within a dense hemlock cover type (Euler and Thurston, 1980; Gates and Harman, 1980). Dense cover immediately above the bed site would also reduce radiant heat loss to the heat sink of a cold, clear night sky (Moen, 1973). Thus, the sites selected for night bedding apparently provided more optimal conditions for survival than the other available sites within the study area.

Night beds selected in the hemlock-northern hardwood forest in western Maryland were similar to those used in Ontario (Armstrong *et al.*, 1983). However, Armstrong *et al.* (1983) found most night beds high up on slopes, especially those facing N. Most night beds in our study area were on nearly level bottomland, where slope was not an important factor. But, in both areas, concentrated hemlock cover was a major factor in common.

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APPENDIX. Microhabitat variables measured at deer beds and random locations within the Blandy Run wintering area

Variable		
Number	Code	Description and methods
1	DECIDBA	Deciduous basal area (m^2/ha) determined with an angle gauge
2	CONIFBA	Coniferous basal area (m^2/ha)
3	TOTALBA	Total basal area (m^2/ha)
4	MAXDENS	Maximum canopy cover (%) determined with a spherical densiometer, Model C (Lemmon, 1956)
5	MINDENS	Minimum canopy cover (%)
6	MEANDENS	Mean ($N = 4$) canopy cover (%)
7-16	(I-V) NE (5 and 10)	Cover density score (Nudds, 1977) northeast (45°) of the sampling point determined at 5 height intervals (I-V) and 2 distances (5 and 10 m). Height intervals are: I, 0-0.5 m;

		II, >0.5-1.0 m; III, >1.0-1.5 m; IV, >1.5-2.0 m; and V, > 2.0-2.5 m. Results represent a single digit "density score" corresponding to a range of quintiles (e.g., 1 corresponds to the range 0-20% cover, 2 to the range 21-40%, etc.)
17-26	(I-V) SE (5 and 10)	Cover density score (Nudds, 1977) southeast (135°) of the sampling point determined at 5 height intervals (I-V) and 2 distances (5 and 10 m)
27-36	(I-V) SW (5 and 10)	Cover density score (Nudds, 1977) southwest (225°) of the sampling point determined at 5 height intervals (I-V) and 2 distances (5 and 10 m)
37-46	(I-V) NW (5 and 10)	Cover density score (Nudds, 1977) northwest (315°) of the sampling point determined at 5 height intervals (I-V) and 2 distances (5 and 10 m)
47	MAXDIST	Maximum distance (m) to the nearest tree (≥7.62 cm DBH) in each of 4 cardinal quadrants centered at the sampling point
48	MINDIST	Minimum distance (m) to the nearest tree in each of 4 cardinal quadrants centered at the sampling point
49	MEANDIST	Mean (N = 4) distance (m) to the nearest tree in each of 4 cardinal quadrants centered at the sampling point
50	HETINDEX	Spatial heterogeneity index of trees at the sampling point (Roth, 1976)
51	IBEAR	Adjusted bearing (°) of the nearest tree in the north (I, >315-45°) quadrant of the sampling point determined with an azimuth compass. The range, >315-45°, was adjusted by subtracting 315° from the true reading if it was >315-360° or by adding 45° to the true reading if it was >0-45°
52	IDIST	Distance (m) to the nearest tree in the north quadrant of the sampling point determined with a metric steel tape or range finder
53	IDBH	DBH (cm) of the nearest tree in the north quadrant of the sampling point determined with a metric diameter tape
54	IIBEAR	Bearing (°) of the nearest tree in the east quadrant (II, >45°-135°)
55	IIDIST	Distance (m) to the nearest tree in the east quadrant
56	IIDBH	DBH (cm) of the nearest tree in the east quadrant
57	IIIBEAR	Bearing (°) of the nearest tree in the south quadrant (III, >135-225°)
58	IIIDIST	Distance (m) to the nearest tree in the south quadrant
59	IIIDBH	DBH (cm) of the nearest tree in the south quadrant
60	IVBEAR	Bearing (°) of the nearest tree in the west quadrant (IV, >225-315°)
61	IVDIST	Distance (m) to the nearest tree in the west quadrant
62	IVDBH	DBH (cm) of the nearest tree in the west quadrant