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Selection of Nesting Habitat by Sharp-tailed Grouse in the Nebraska Sandhills

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ABSTRACT -- We evaluated nesting habitat selection (disproportionate use compared to availability) by plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi*) on rangelands grazed by cattle (*Bos taurus*) relative to height, density, and heterogeneity of residual herbaceous vegetation remaining from previous growing seasons. Residual cover is critical for nesting sharp-tailed grouse and can be lacking on grazed rangelands. Aerial photography and a geographic information system were used to analyze residual cover height classes and several measures of residual cover heterogeneity in nest (n = 38) and random (n = 38) plots. Height classes corresponded to visual obstruction readings (VORs), the height to which total visual obstruction by vegetation occurs. Analyses were conducted for five spatial scales ranging from 1 to 16 ha to test for scale effects on nesting habitat selection. Sharp-tailed grouse selected nesting habitat with more area in tall (greater than or equal to 4 cm VOR) residual cover than at random sites at all scales, less area in short residual cover (less than 2 cm VOR) at the 1-ha scale, and less area in short and medium (2 to 3.9 cm VOR) residual cover at the 2-through 16-ha scales. Selection of shrub habitat containing patches of shrubs was evident only at the 16-ha scale. Patches of tall residual cover were larger in nest plots than in random plots at the 8- and 16-ha scales, and patches of short cover were smaller in nest plots at the 1-ha scale. Two scales of pattern defined by mean patch size were detected for overall residual cover, but did not relate to nesting habitat selection.

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Key words: aerial photography, habitat selection, Nebraska, nesting, patchiness, sharp-tailed grouse, spatial scale, *Tympanuchus phasianellus*.

Height and density of residual cover, dried herbaceous vegetation remaining from previous growing seasons, during spring are often used as predictors of nesting cover quality for sharp-tailed grouse (*Tympanuchus phasianellus*) (Kohn 1976, Rice and Carter 1982, Messmer 1985, Manske and Barker 1988). Residual cover is critical because little new growth is available in early spring when sharp-tailed grouse begin nesting, and it can provide much of the cover throughout the nesting season during drought years. Inadequate height and density of residual cover is the most commonly cited limiting factor for plains sharp-tailed grouse (*T. p. jamesi*) throughout its range (Kessler and Bosch 1982). Recommendations for suitable height and density of nesting cover have been developed for management of plains sharp-tailed grouse habitat in North Dakota (Christenson 1970, Kohn 1976, Manske and Barker 1988). These quantitative standards, developed from habitat use studies, were intended to ensure that habitats remained suitable for sharp-tailed grouse under various land uses, such as grazing. However, vegetation structure across the sharp-tailed grouse's range varies because of differing soil types, plant communities, and rangeland uses. Thus, standards for nesting cover in other parts of the sharp-tailed grouse's range might not be applicable to the Nebraska Sandhills.

The influence of spatial scale and vegetation heterogeneity on habitat use by sharp-tailed grouse is not well understood. Habitat use by birds is scale-dependent and can occur through a sequence of hierarchical scales (Hildén 1965, Wiens 1989). If the spatial scale at which habitat use is studied is dissimilar to the scale at which habitat use decisions are made, relationships between habitat-use patterns and measured habitat variables could be overlooked or misinterpreted (Wiens 1989). Although apparent preference for taller nesting cover is well documented for sharp-tailed grouse, use of cover relative to different spatial scales rarely has been considered. The spatial scales at which cover conditions influence use of nesting habitat could be an important consideration for habitat management, especially where cattle (*Bos taurus*) grazing is a likely disturbance to grasslands.

Heterogeneity in vegetation structure has been identified as a factor in habitat use by birds (Wiens 1974, Cannon and Knopf 1981, Messmer 1985, Freemark and Merriam 1986), but measures of heterogeneity are often disregarded in favor of mean values of vegetation structure, such as height and density, for habitat studies and management recommendations. If the influence of habitat heterogeneity on habitat use can be ascertained, measures of heterogeneity might help refine management criteria.

We compared use and availability of nesting habitat by sharp-tailed grouse in

the Nebraska Sandhills during the 1989 breeding season to ascertain patterns of habitat selection³, and infer a relationship between height and density of residual cover and nesting habitat suitability. We focused on two factors often neglected in studies of habitat use: spatial scale and vegetation heterogeneity. If birds select habitats that maximize their fitness (Hildén 1965, Pianka 1988:182), nesting habitat selection by sharp-tailed grouse should serve as an indication of habitat suitability and guide for management recommendations.

STUDY AREA

The Bessey District of Nebraska National Forest (NNF) is located in Thomas County, 97 km north of North Platte, Nebraska. About 85% of the 360-km² district is native grassland of the Nebraska Sandhills Prairie community type (Küchler 1964). The remaining area is conifer plantation, primarily ponderosa pine (*Pinus ponderosa*), jack pine (*Pinus banksiana*), and eastern redcedar (*Juniperus virginiana*). The study area was limited to about 11,500 ha of grassland on the western half of the district. Linear sand dunes stabilized by vegetation are the predominant topographic feature. These dunes are generally aligned in a northwest to southeast direction and form two predominant range sites: Sands and Choppy Sands (U.S. Soil Cons. Serv. 1965).

The Sands range site is characterized by nearly level to rolling dunes (3 to 16% slope), whereas, the Choppy Sands range site has high, steep dunes (greater than 16% slope) with sharp peaks and ridges. Bunchgrasses were the predominant vegetation, with little bluestem (*Schizachyrium scoparium*) as the most abundant species. Other bunchgrasses were sand bluestem (*Andropogon hallii*), sand lovegrass (*Eragrostis trichodes*), switchgrass (*Panicum virgatum*), and prairie sandreed (*Calamovilfa longifolia*). Annual eriogonum (*Eriogonum annuum*), western ragweed (*Ambrosia psilostachya*), and pricklypear (*Opuntia* spp.) were common forbs. Common woody species were wild rose (*Rosa* spp.), leadplant (*Amorpha canescens*), sand cherry (*Padus pumilia*), small soapweed (*Yucca glauca*), New Jersey tea (*Ceanothus herbaceus*), choke cherry (*Padus virginiana*), wild plum (*Padus americana*), and western snowberry (*Symphoricarpos occidentalis*). A more complete list of plants has been compiled by Sisson (1976).

Annual cattle grazing occurred on most of the study area under a permit system. The primary grazing system was deferred rotation involving two to five pastures during the summer growing season, beginning 15 May to 1 June. Stocking rates averaged 1.2 ha per AUM (animal unit month) during the study. Some winter and spring grazing also occurred during the study. A 283-ha research reference area that had been ungrazed for several years was located within the

³Disproportionate use compared to availability (Manly et al. 1993).

study area.

METHODS

The objectives of our study posed several problems for sampling. Firstly, testing for effects of spatial scale required sampling large areas to include a broad range of scales. Secondly, accurate measurements of residual cover required a snow-free period prior to new spring growth, which limited sampling to a five- to six-week window beginning in early April. Thirdly, sharp-tailed grouse nests are difficult to locate until females began incubation, as the females are mobile during the nest-building and egg-laying periods and tend not to sit on the nests until incubation begins. By this time, new growth of vegetation would have obscured residual cover at some nests, which made accurate measurements of residual cover impossible. Lastly, human activity around occupied nests could have disturbed nesting hens and attracted predators to the nests. We addressed these problems by using aerial photography to provide a record of vegetation over the entire study area during the narrow window of appropriate conditions, and conducting assessments of vegetation around nests by using aerial photograph imagery. This approach eliminated disturbance that would have occurred around nests during the extensive field measurements that, otherwise, would have been necessary for the study design.

We assessed habitat selection by comparing plots with known sharp-tailed grouse nests with random plots (use and availability). Several variables were used to describe vegetation structure and heterogeneity within the plots. We conducted assessments at five nested plot sizes to test for effects of spatial scale. Additional tests compared patchiness (i.e., patch size and spatial pattern) of vegetation between nest plots and random plots.

Delineating vegetation conditions in nest and random plots from aerial photographs was a two-step process. First, we ground checked aerial photographs to calibrate visual interpretation of photograph images (Ebert and Lyons 1983). This was done by collecting field data in reference plots on the ground and referencing the data to aerial photograph images to identify vegetation signatures, which are visual characteristics in photographs from which vegetation structure can be identified. Signatures were then extrapolated to nest and random plots on the aerial photographs to quantify vegetation variables.

During mid-April, 1989, we established 30 X 100-m reference plots; nine in Sands range sites and nine in Choppy Sands. We distributed reference plots to cover the range of residual cover heights and densities expected to occur on the study area, as estimated from vegetation surveys conducted during spring, 1988 (Prose 1992). Long sides of plots were aligned perpendicular to sand dune ridges to sample across these linear features. Corners and the middle of long sides were

marked with 3 X 6-m sheets of plastic-coated freezer paper scoured flat on the ground with 18-cm nails and twine (Francis and Kerbs 1984). The markers directed aerial photographers to reference plots and defined plot boundaries on aerial photographs.

We visually delineated vegetation patches in reference plots based on height and density of residual cover and plant species composition. Patches were mapped as polygons. We used visual obstruction readings (VORs) (Robel et al. 1970), a commonly used method to quantify nesting cover for upland-nesting birds (Rice and Carter 1982, Messmer 1985, Manske and Barker 1988), to measure the concealment provided by height and density of residual vegetation. VOR poles were round, 3 cm in diameter, and graduated in 2-cm light gray and white bands beginning with 0 cm.

We recorded VORs every 1 m along transects through the centers of residual cover patches in the direction of the patches' longest dimensions. For patches wider than 3 m, parallel transects were 1 m apart. We did not record VORs for shrub patches. A reading was taken from the east and west at each sample point and averaged. We recorded readings as the last 2-cm bands completely obscured by vegetation, and took them between 0800 and 1500 CST to minimize shadows on the pole caused by low sun angles. Only visual obstruction from residual cover was considered in readings, except where thin shrubby material was intermixed, which made strictly herbaceous readings impossible. We qualitatively recorded plant species abundance and color and coverage of soil for each patch.

Aerial photographs were taken in mid-April from a fixed-wing aircraft equipped for image motion compensation. We photographed reference plots at a scale of 1:1000, and the entire study area at a scale of 1:8000. Aerial photographs were 23 X 23-cm color infrared transparencies, exposed through a number 12 Wratten filter. Aerial photography was completed in a single day to eliminate effects of day-to-day variation in light and atmospheric conditions, and between 1000 and 1300 CST to minimize shadows. To supplement aerial photographs, we photographed patches in each reference plot by using 35-mm color and color infrared films at both vertical and oblique angles from a 2.5-m stepladder.

We identified vegetation signatures to differentiate residual cover from woody vegetation and estimate VOR of residual cover on the aerial photographs. We viewed reference plots on both 1:1000- and 1:8000-scale photographs with a zoom stereoscope at 10X magnification, and identified visual characteristics (signatures) that were diagnostic of the vegetation structure recorded in the field. We used an iterative process, which analyzed six reference plots at a time to develop and test signatures. Diagnostic information acquired at each iteration was applied to the next set of six reference plots to refine vegetation signatures.

We identified signatures for four vegetation classes: short, medium, and tall residual cover and shrubs. Short, medium, and tall classes for residual cover corresponded to mean VOR ranging 0.0 to 1.9 cm, 2.0 to 3.9 cm, and greater than or

equal to 4 cm, respectively. The shrub class included all shrubby vegetation forming dense patches. Small individual shrubs and sparse patches could not always be distinguished on photographs.

Nest locations were provided by the Nebraska Game and Parks Commission (NGPC) and NNF, who had trapped and radio-marked hens on display grounds for a concurrent study of nest micro-habitat and nesting chronology. When nesting was completed (late June), we visited 38 nest sites and marked them on the 1:8000-scale aerial photographs, which were representative of vegetation conditions during April. Square 16-ha plots (400 m X 400 m) were centered around each of the 38 nest sites and 38 random points selected from a grid of contiguous 16-ha plots mapped over the study area. We chose 16 ha for the maximum plot size because we assumed it would encompass most of the area in which nesting females obtained resources during laying and incubation (Gratson 1988:172), and most of the area used by broods during the first few days after hatching (Pepper 1972). We delineated vegetation in nest and random plots into the residual cover height classes and shrub cover according to signatures derived from reference plots. The minimum mapping unit was 100 m². We digitized vegetation patches in nest and random plots into a geographic information system (GIS) to determine patch areas for short, medium, and tall residual cover height classes and shrub cover (Prose 1992:39-44).

We evaluated spatial patterns of residual cover height classes by using the New Local Variance (NLV) method (Galliano 1982), a form of hierarchical ANOVA. This method describes pattern as mean width and spacing of vegetation patches, and can identify multiple scales of pattern (i.e., small patches nested within larger patches). NLV analyses used 128 X 128-cell grids overlaid on the 38 16-ha nest plots and 38 16-ha random plots (Prose 1992:41). Data handling was facilitated by using GIS utilities. Shrubs were omitted from NLV analysis because VORs were not measured for shrubs.

We analyzed nesting habitat use and availability by comparing distributions of nest and random plots with multiresponse permutation procedures (MRPP; standardized test statistic = T) (Zimmerman et al. 1985, Mielke and Berry 2001). Sample sizes for all statistical tests were 38 nest plots and 38 random plots. Our analyses involved two main classes of comparisons: cover class composition (i.e., proportions of short, medium, and tall residual cover and shrub cover) and measures of cover patchiness. Multivariate comparisons of cover composition were made with variables standardized by their average Euclidean distances. This yields more powerful MRPP analyses than standardizing by the variance/covariance matrix (e.g., as is done in Hotelling's T²) when distributional differences among groups are primarily parallel to the major axes of covariation among the multiple variables (Mielke and Berry 1999). We examined patterns of covariation among multiple dependent variables for nest sites and random sites by superimposing multidimensional scatter plots over multivariate medians (Berry and Mielke

1984), and by comparing changes in parallel coordinate plots.

We initially conducted compositional analyses to detect effects of spatial scale by using univariate comparisons, where nested subplots of 1, 2, 4, 8, and 16 ha were considered interdependent repeated measures. We used differences between all possible pairs of nested subplots simultaneously in a multivariate repeated measures design (Looney and Stanley 1989) to test for interaction of subplot size and use-availability effect (Baker et al. 1995). Differences occurring between nest and random plots at one or more subplot sizes, but not at all sizes, would indicate a scale effect. We then made multivariate tests for differences in vegetation composition between nest and random plots by using different subsets of cover variables (i.e., short, medium, and tall residual cover and shrub cover) at different spatial scales. Cover variables tested were based on the univariate differences, as described above, shifts in multivariate medians, and patterns of covariation identified by multidimensional scatter plots and parallel coordinate plots. Our analyses of residual cover selection were structured to accommodate the inherent compensation that must occur with compositional variates (i.e., greater use of any component must be accompanied by less use of some other component(s)).

Because MRPP is sensitive to distributional differences in central tendency and dispersion, we used Van Valen's test (Van Valen 1978) to examine the influence of multivariate dispersion differences. Van Valen's test is equivalent to a multivariate extension of Levene's test (Conover et al. 1981), where Euclidean distances between observations and multivariate medians of nest or random plot group were compared with a permutation version of a t-test of equality of means. Using MRPP allowed us to determine whether dispersion could be eliminated as a cause of distributional differences detected by multivariate comparisons of cover composition.

Patch edge, distance from center of plot to nearest tall residual cover or shrubs, average patch width identified by NLV, and average size and number of patches of short, medium, tall residual cover, and shrub cover were compared between nest and random plots with univariate MRPP. To emulate a continuous measure of VOR similar to that obtained by field sampling, we created a composite variable, mean effective height (MEH), that was a weighted average of midpoints of mean VOR ranges associated with short, medium, and tall residual cover classes. Relative probabilities of different MEHs being selected for nesting by sharp-tailed grouse were estimated by using a selection function (McDonald et al. 1990). Relative probabilities were derived from a logistic regression of plot type (i.e., nest or random), which was the dependent variable, and MEH, which was the independent variable. Parameters of the logistic regression function were estimated by maximum likelihood, and the P-value for the null hypothesis $\beta = 0$ was evaluated by LOGXACT permutation procedures (Mehta and Patel 1993).

RESULTS

Nesting habitat selected by sharp-tailed grouse had more tall (greater than or equal to 4 cm VOR) residual cover at all spatial scales, with weaker differences at the 1-ha scale (Fig. 1); however, little evidence of an interaction existed between subplot size and use-availability effect ($T = -1.016$, $P = 0.134$). Percent area in short (less than 2 cm VOR) cover was lower in nest plots than random plots at the 1- and 2-ha scales (Fig. 2). Less difference in percent short cover occurred at the 4-ha scale, and no differences occurred at the 8- and 16-ha scales. This was consistent with an interaction between subplot size and use-availability effect for percent short cover ($T = -1.714$, $P = 0.066$). Percent area in medium (greater than 2 cm and less than 4 cm VOR) cover was lower in nest plots (82%) than random plots (87%) at the 16-ha scale ($T = -1.415$, $P = 0.088$), but differed little between nest and random plots at scales smaller than 16 ha ($T = 0.868$, $P = 0.379$; $T = -0.429$, $P = 0.226$; $T = -0.794$, $P = 0.160$; $T = -0.900$, $P = 0.145$ for 1-, 2-, 4- and 8-ha plots, respectively). Percent area in shrub cover was greater in nest plots (2%) than random plots (1%) at the 16-ha scale ($T = -1.047$, $P = 0.124$), but sharp-tailed grouse showed little response to percent area in shrubs at scales smaller than 16 ha ($T = 0.591$, $P = 0.664$; $T = 0.817$, $P = 0.379$; $T = 0.473$, $P = 0.580$; $T = 0.434$, $P = 0.552$ for 1-, 2-, 4-, and 8-ha plots, respectively).

Multivariate tests for differences in composition of vegetation classes (i.e., short, medium, and tall residual cover and shrub cover) showed no evidence that multivariate dispersions differed between nest and random plots at any scale (Table 1). Thus, all differences in cover composition were inferred to be shifts in multivariate medians between nest and random plot data distributions. At the 16-ha scale, sharp-tailed grouse selected plots with less medium and more tall residual cover, and more shrub cover than random plots. At the 8-ha scale, nest plots had less medium and more tall residual cover. Nest plots had less short, less medium, and more tall residual cover at the 4-ha scale, and less short, less medium, and more tall residual cover at the 2-ha scale. At the smallest scale of 1-ha, nest plots had less short and more tall residual cover. Although nest plots had only 3 to 6% more tall cover than random plots across scales, this was double the area in tall cover (Table 1).

Differences in proportions of short and tall residual cover in nest and random plots were related to differences in average patch sizes. Proportion of tall residual cover was correlated with average patch size of tall cover ($r = 0.81, 0.73, 0.80, 0.85, 0.85$ for 1-, 2-, 4-, 8-, and 16-ha scales, respectively), and proportion of short residual cover was correlated with average patch size of short cover ($r = 0.90, 0.82, 0.73, 0.71, 0.75$ for 1-, 2-, 4-, 8-, and 16-ha scales, respectively). Patches of tall cover were larger in nest plots than random plots at the 2-, 8-, and 16-ha scales of analysis, but not at the 1- or 4-ha scales (Fig. 3). This was consistent with an

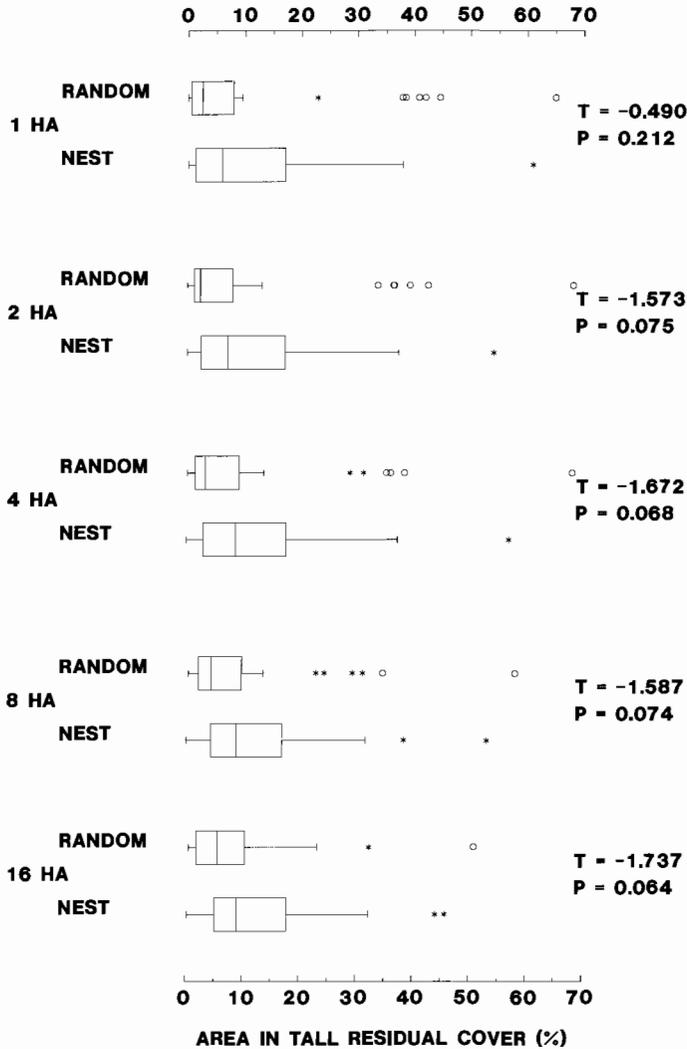


Figure 1. Mean percent area of tall (≥ 4 cm VOR) residual cover in relation to nest and random plots on Bessey District of Nebraska National Forest, 1989. Effects of spatial scale illustrated by sizes of nested plots used in analysis. Probabilities from MRPP comparisons between nest ($n = 38$) and random ($n = 38$) plots. Center vertical line in box is median, box is interquartile range (25th-75th percentile), whiskers are values ≤ 1.5 X interquartile range, asterisks are values greater than 1.5 X interquartile range, and open circles are values greater than 3 X interquartile range.

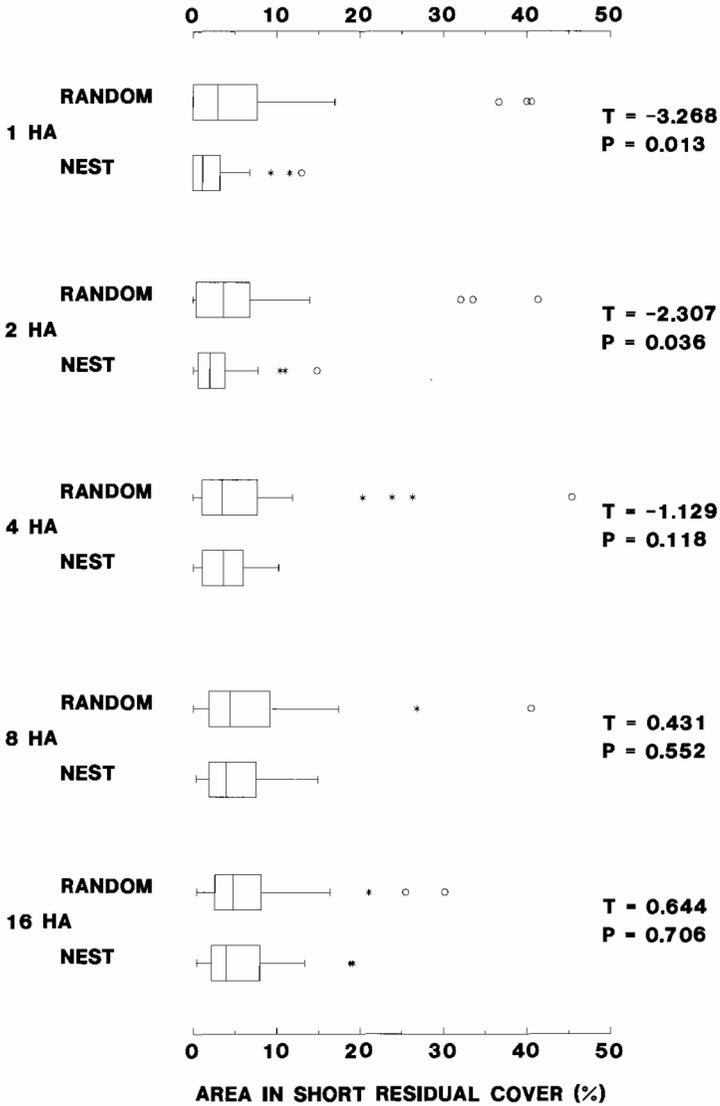


Figure 2. Mean percent area of short (< 2 cm VOR) residual cover in relation to nest and random plots on Bessey District of Nebraska National Forest, 1989. Effects of spatial scale illustrated by sizes of nested plots used in analysis. Probabilities from MRPP comparisons between nest (n = 38) and random (n = 38) plots. Symbols defined in Figure 1.

Table 1. Estimates of multivariate medians for composition (percent area) of short (less than 2 cm VOR), medium (2 to 3.9 cm VOR), and tall (greater than or equal to 4 cm VOR) residual cover, and shrub cover and average absolute deviations from estimates used to compare sharp-tailed grouse nest (n = 38) and random (n = 38) plots at five nested spatial scales on Bessey District of Nebraska National Forest, 1989. Probabilities are for omnibus test of distributional differences with MRPP and for Van Valen’s test of dispersion made with permutation t-test of equality of mean absolute deviations from multivariate medians.

Spatial Scale	Plot Type	Residual Cover			Shrub Cover	Average Deviation	MRPP T, P	Van Valen T, P
		Short	Medium	Tall				
1 ha	Nest	1.5		6.6		9.3		
	Random	4.2		3.6		13.0	-2.542, 0.026	-0.335, 0.241
2 ha	Nest	2.4	87.3	8.9		13.0		
	Random	5.1	91.0	3.3		17.3	-2.255, 0.037	0.016, 0.351
4 ha	Nest	3.9	85.9	8.5		12.3		
	Random	5.5	89.3	3.9		16.1	-1.679, 0.069	0.005, 0.352
8 ha	Nest		84.0	9.2		11.5		
	Random		88.2	4.8		12.4	-1.183, 0.109	0.701, 0.756
16 ha	Nest		82.3	10.1	2.1	11.7		
	Random		86.5	5.9	1.5	10.8	-2.524, 0.028	0.697, 0.748

interaction between subplot size and use-availability effect (T = -3.538, P = 0.008). Patches of short residual cover were smaller in nest plots than random plots at the 1-ha scale, but were larger in nest plots at the 4-ha scale (Fig. 4). Tests for interaction of subplot size and use-availability effect were inconclusive (T = -0.178, P = 0.298), possibly due to confounding of interaction caused by smaller patches of short cover shifting from nest plots to random plots (and the reverse for larger patches) between the 1- and 4-ha subplot sizes. Because medium-height cover rarely formed patches, we did not analyze patch-related variables for this residual cover height class. Average patch size of shrubs was larger in nest plots than random plots at the 2- and 16-ha scales (T = -1.084, P = 0.117 and T = -1.416, P = 0.088, respectively), with little evidence of differences at other scales (T = 0.391, P = 0.577; T = -0.367, P = 0.241; T = 0.126, P = 0.410 for 1-, 4-, and 8-ha scales, respectively). Selection was not influenced at any scale by amount of patch edge (T = -0.994, P = 0.338; T = 0.311, P = 0.479; T = -0.008, P = 0.347; T = -0.679, P = 0.177;

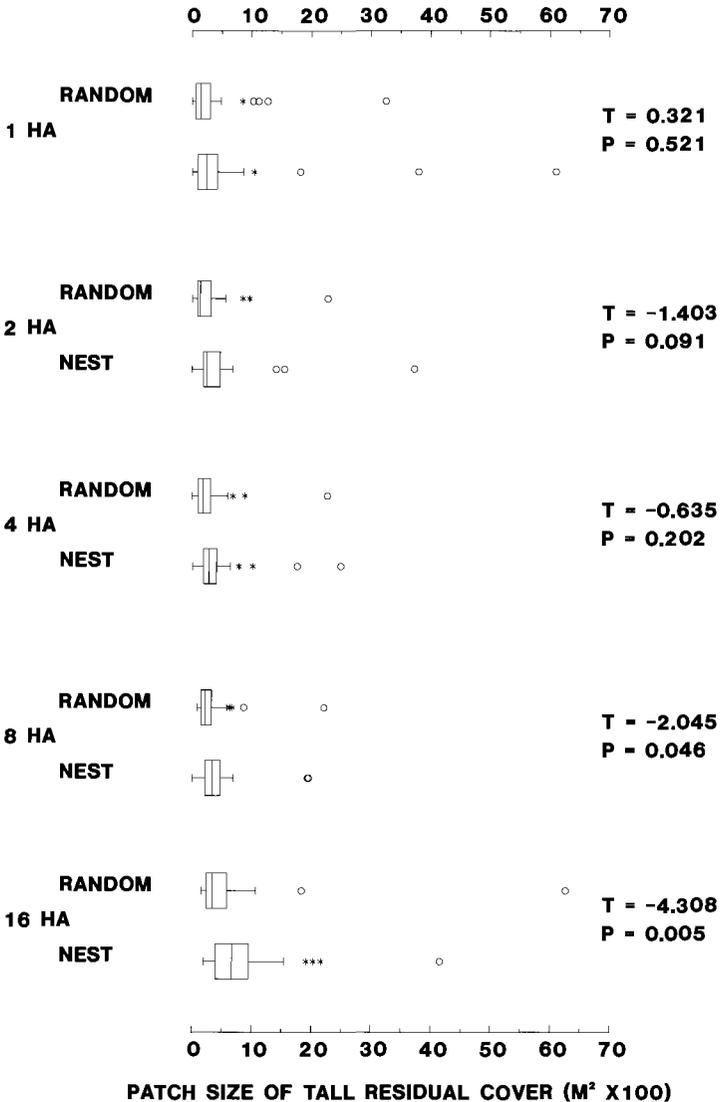


Figure 3. Mean patch size of tall (≥ 4 cm VOR) residual cover in relation to nest and random plots on Bessey District of Nebraska National Forest, 1989. Effects of spatial scale illustrated by sizes of nested plots used in analysis. Probabilities from MRPP comparisons between nest ($n = 38$) and random ($n = 38$) plots. Symbols defined in Figure 1.

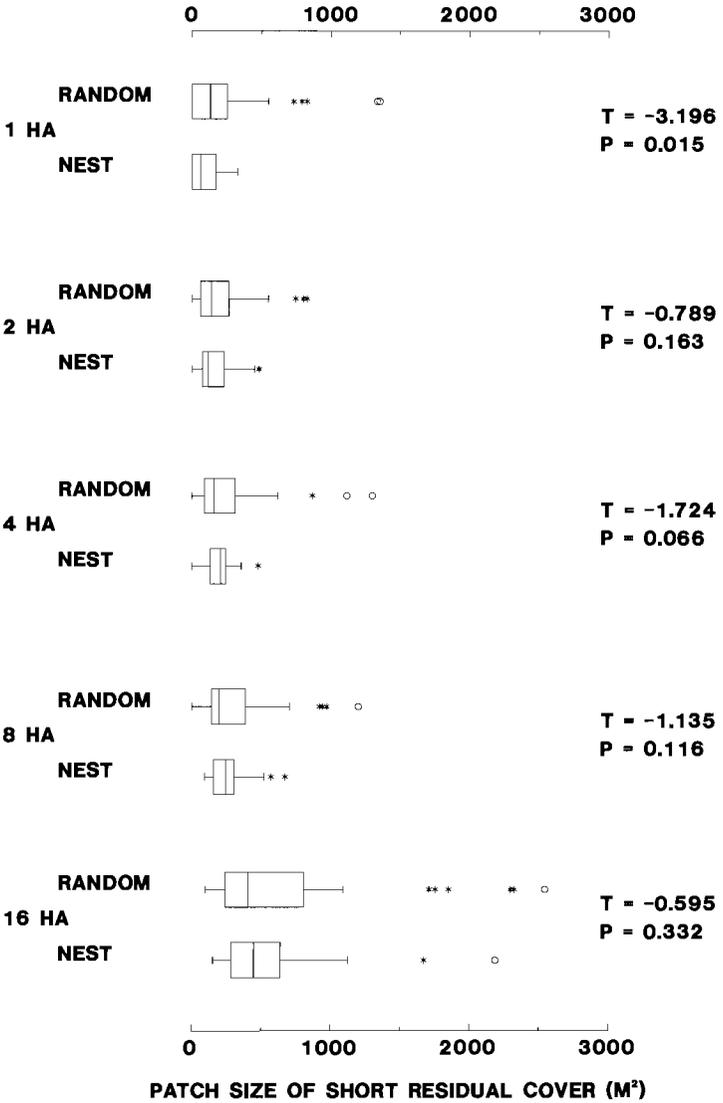


Figure 4. Mean patch size of short (< 2 cm VOR) residual cover in relation to nest and random plots on Bessey District of Nebraska National Forest, 1989. Effects of spatial scale illustrated by sizes of nested plots used in analysis. Probabilities from MRPP comparisons between nest (n = 38) and random (n = 38) plots. Symbols defined in Figure 1.

$T = -0.495$, $P = 0.215$ for 1-, 2-, 4-, 8-, and 16-ha scales respectively), nor at 16-ha cover scale (only scale measured) by distance between nests and nearest patches of tall residual ($T = 0.618$, $P = 0.687$), shrubs ($T = -0.491$, $P = 0.212$), or either tall cover or shrubs ($T = 0.191$, $P = 0.429$).

Two scales of pattern (mean patch width) among residual cover classes were detected in most 16-ha nest plots and random plots by using NLV, but the scales of pattern (averaging 23.4 m and 162.5 m in nest plots and 23.5 m and 161.0 m in random plots) did not differ between plot types ($T = 0.746$, $P = 0.800$ and $T = -0.566$, $P = 0.202$ for small and large scales, respectively). A bivariate MRPP test for both scales together also showed no indication of selection for residual cover pattern ($T = -0.181$, $P = 0.385$).

DISCUSSION

Vegetation in nest and random plots generally occurred as patches of tall and short residual cover and shrubs, within a background of medium-height residual cover that was typically greater than 80% of the plot area. The short residual cover class had less cover of little bluestem and greater cover of ragweed, wild rose, and leadplant compared to medium and tall cover classes. Frequent bare ground and scattered clumps of vegetation in this bunchgrass community resulted in much lower VORs than reported in other studies, where sod-forming grassland communities provided more uniform cover. However, differences in vegetation height and density were visually distinct in the field and distinguishable on aerial photographs. Because Sandhills shrubs are often small, sparsely-stemmed, and intermingled with residual cover, particularly wild rose and leadplant, our VORs for residual cover might reflect shrubby material to a greater degree than VORs in other studies.

The substantially lower VORs measured on our Nebraska Sandhills study area compared to those reported in other portions of the plains sharp-tailed grouse's range highlight the considerable differences in vegetation structure between bunchgrass and sod-forming communities. These differences indicate that vegetation management standards are not interchangeable among different community types, and that management standards designed specifically for the Nebraska Sandhills are needed.

Selection for nesting habitat having relatively greater proportions of tall, dense residual cover was consistent with previous studies in the Nebraska Sandhills, where females tended to use lightly-grazed or ungrazed areas for nesting (Kobriger 1964, Blus and Walker 1966, Sisson 1976). However, these studies were not sensitive to spatial scale of habitat use. Sharp-tailed grouse selection for greater proportions of tall (greater than 4 cm VOR) residual cover at all spatial scales evaluated in our study indicated that relatively tall, dense residual cover

was a major component of nesting cover for at least 16 ha (the largest scale evaluated) surrounding nests. Because the area in tall residual grass cover at nest sites was about twice that at random sites across all spatial scales, apparently, sharp-tailed grouse in grazed Nebraska Sandhills are making the best of limited available tall cover. Our study was not designed to specifically compare grazed and ungrazed areas, but nesting sharp-tailed grouse did not appear to disproportionately use NNF's research reference area, which had not been grazed or burned since the early 1950s (G. L. Schenbeck, NNF, personal communication). We speculate from general observations that brood habitat suitability might have been less than optimum on this area because of apparent reduced abundance of forbs and invertebrates. Had absence of disturbance been shorter-term, we would have expected greater use of the area by nesting sharp-tailed grouse.

Although our study did not evaluate cover at the immediate nest site, NGPC and NNF found during their related study of nest micro-habitat that nests of sharp-tailed grouse occurred within patches of tall cover (W. L. Vodehnal, NGPC, and G. L. Schenbeck, NNF, unpublished data). Their field measurements within 3 to 12 m of a subset ($n = 23$) of the same nests analyzed in our study, produced a mean VOR of 4.2 cm (equivalent to our tall residual cover class). This was consistent with nesting cover use by sharp-tailed grouse in other parts of its range, where they tended to use relatively tall, dense vegetation at nests (Brown 1968, Pepper 1972, Kohn 1976, Messmer 1985, Grosz 1988).

Weak indications of selection for tall, dense shrubby cover was contrary to habitat use by prairie sharp-tailed grouse (*T. p. campestris*) in Wisconsin and Michigan (Hamerstrom 1939, Ammann 1957), and could be due to shrub scarcity on our study area. Bergerud and Gratson (1988:525) suggested that, where shrubs were rare and conspicuous, grouse should avoid nesting under them and instead "attempt to become lost in a sea of grass" to guard against nest predators. This view is substantiated by Christenson (1970), who found that predators of sharp-tailed grouse nests in North Dakota appeared to key on isolated habitat features. Nest predation was high for sharp-tailed grouse that were forced, by heavy grazing, to nest in and near shrubby draws, which were thought to be predator lanes (Christenson 1970).

Evaluation of spatial pattern and patchiness was intended to detect vegetation structures that might be selected by nesting sharp-tailed grouse. Interpretation of results for spatial pattern of residual cover was uncertain because of correlations between mean patch size and percent area of cover classes. Nesting sharp-tailed grouse appeared to select habitat where short cover near nests (1-ha scale) occurred in smaller patches, but smaller patches occurred in areas where percent area of short cover was relatively low. Similarly, sharp-tailed grouse appeared to select for large patches of tall cover greater than 50 m from nests (2-, 8- and 16-ha scales), but patches of tall cover were larger in areas where percent area of tall cover was greatest. Thus, we could not separate the influences of patch size

and overall percent area of these cover classes on nesting habitat selection.

A habitat suitability relationship was developed from plotting cumulative frequency of nests relative to MEH at the 16-ha scale of analysis (the largest scale evaluated) (Fig. 5). This relationship is similar to that developed by Prose (1987) based on sharp-tailed grouse data from other parts of its range, but is designed specifically for vegetation structure of the Nebraska Sandhills. The relationship is based on our premise that sharp-tailed grouse should select the most suitable habitat available (i.e., that which provides for greatest fitness (Hildén 1965, Pianka 1988)). The suitability relationship is supported by a selection function (McDonald et al. 1990) for sharp-tailed grouse nest habitat at the 16-ha scale, which indicated that the relative probability of an MEH being selected for nesting increased monotonically with increasing MEH (Fig. 6). The probability of a 16-ha plot being a nest plot increased by a factor of 4.5 (90% CI = 1.01-22.41, $P = 0.099$) for each 1-cm increase in MEH, e.g., plots with MEH of 3.0 were 4.5X more likely to be a nest plot than a random plot, compared to plots with MEH = 2.0 cm (Fig. 6).

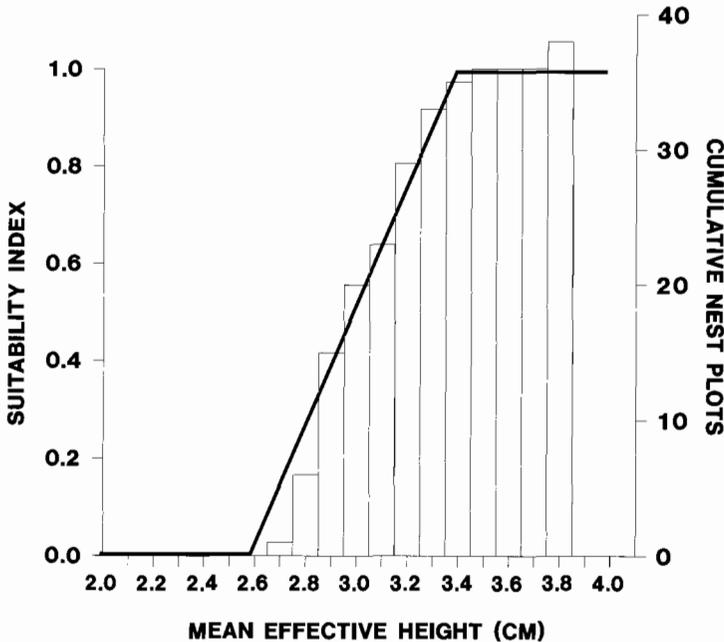


Figure 5. Relationship between mean effective height of residual cover and nesting habitat suitability for plains sharp-tailed grouse on Bessey District of Nebraska National Forest. Suitability curve based on cumulative number of nest plots ($n = 38$) in respect to mean effective height of residual cover.

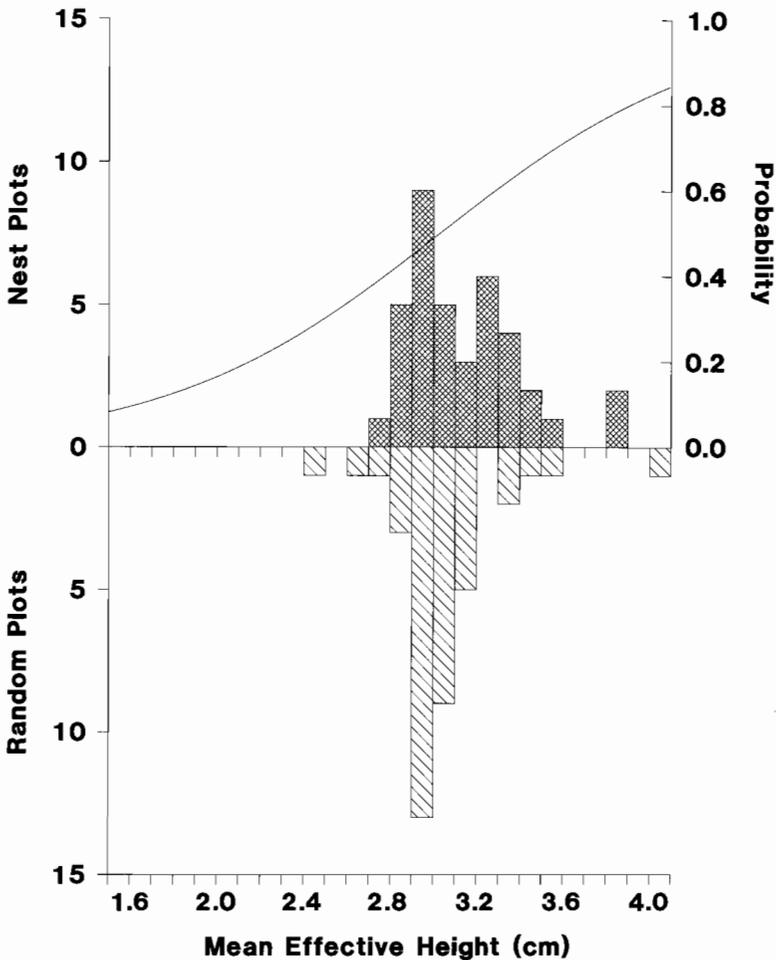


Figure 6. Relative probability of mean effective height selection by plains sharp-tailed grouse on Bessey District of Nebraska National Forest. Probability curve derived from permutation version of logistic regression ($b_1 = 1.504$, 90% CI = 0.01-3.11, $P = 0.099$) for nest plots ($n = 38$) and random plots ($n = 38$), and is superimposed on distributions of plot frequencies. MEH is weighted average of short, medium, and tall residual cover class mid-points.

Nesting cover is generally considered the most frequent limiting factor for plains sharp-tailed grouse (Kessler and Bosch 1982) and, therefore, the relationship might be useful for comparing habitat areas and developing management standards

for grasslands within the Nebraska Sandhills. However, the suitability relationship reflects response of nesting females only to the range of vegetation conditions on the study area at the time, and does not imply that an MEH of 4 cm represents maximum suitability for sharp-tailed grouse throughout the Nebraska Sandhills. We cannot speculate whether, or at what point, suitability eventually should decline if MEH increased beyond that encountered in our study plots. The limited data for MEH higher than about 3.4 cm precluded any possibility of detecting selection for, or avoidance of, MEH beyond the range depicted in the suitability relationship (Fig. 5). Climate and grazing practices influence height, density, and spatial pattern of vegetation, and should be considered when applying the suitability relationship to other locations or in other years. Because most of the study area was grazed by livestock, the relationship is most appropriate for assessing similarly grazed Nebraska Sandhills habitats.

ACKNOWLEDGMENTS

Our study was funded and supported by the Midcontinent Ecological Science Center of the U.S. Geological Survey (formerly National Ecology Research Center of the U.S. Fish and Wildlife Service). G. L. Schenbeck and the Nebraska National Forest provided the opportunity to conduct the study and contributed technical support. We thank J. Mitchell, W. L. Vodehnal, and the Nebraska Game and Parks Commission for providing the nest locations used for our study. R. S. Driscoll, R. J. Myhre, and C. Sumpter advised on aerial photography. We also thank B. W. Baker, J. W. Terrell, and three anonymous reviewers for *The Prairie Naturalist* for reviews of draft manuscripts.

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Received: 22 December 2000

Accepted: 22 June 2002