TERRITORY SIZE VARIATIONS IN SHRUBSTEPPE BIRDS

JOHN A. WIENS,[1] JOHN T. ROTENBERRY,[2] AND BEATRICE VAN HORNE[1]

[1]*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA, and*
[2]*Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA*

ABSTRACT.—We recorded variations in sizes of breeding territories of Sage (*Amphispiza belli*) and Brewer's (*Spizella breweri*) sparrows at four locations in shrubsteppe habitats during 1976–1983. There was considerable variation in territory sizes of both species, and ANOVA tests indicated that site, plot within site, and year all contributed to this variation. Territory-size variations of Sage Sparrows were correlated with differences in several habitat features, while those of Brewer's Sparrows showed no relation to habitat variation. Territory sizes in both species varied inversely with breeding population densities, although in different ways. Our findings cast doubt on the meaning or value of "average" territory-size measures for a species as a whole. *Received 31 August 1984, accepted 29 November 1984.*

MEASUREMENTS of the sizes of breeding territories of birds figure importantly in a variety of theoretical and applied considerations. For example, territory size often bears a relationship to body size in a manner that varies as a function of the food habits of the organisms (Schoener 1968, Peters 1983). One may wish to use such relationships to predict the area required by an individual or by a population of a certain size from body mass; such information may be useful in projecting the necessary size of a natural reserve for a species.

These patterns are based upon comparisons among species spanning several orders of magnitude in body mass. Territory size also varies among individuals within a species (e.g. Wiens 1969, 1973), however, and these variations are also of interest. Such differences, for example, may index habitat quality, as individuals occupying poorer habitats may have to establish larger territories to obtain sufficient resources. Territory size also may be related to mating status, with individuals defending larger territories having an enhanced probability of attracting multiple mates in polygynous species. There are likely to be upper and lower limits to territory size within a species, determined by the economic defensibility of the territory and the resources it contains (Brown 1964, Gill and Wolf 1975, Carpenter and MacMillen 1976).

To test such ideas requires information on both territory sizes and resources. Although the former may be measured with relative ease, the latter is difficult to obtain in many situations (Wiens 1984). In the absence of resource measurements, insights into the dynamics of territory-size variations may be obtained from comparisons with other proximate correlates. In this paper we analyze territory size and its variations in two common species of shrubsteppe birds and explore its relationship to population densities and features of breeding habitats.

METHODS

We conducted our studies at four sites in semiarid shrubsteppe environments of Washington, Oregon, and Nevada during the period 1976–1983: the ALE site, located in the Columbia River basin in southeastern Washington; the Cabin Lake and Fort Rock sites, situated within 20 km of each other in the northwestern extension of the Great Basin in central Oregon; and the Star Creek site, in the central Great Basin in north-central Nevada. Details of these locations and our sampling procedures have been presented elsewhere (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Wiens et al. MS). At each site we established two 9-ha gridded plots surrounded by large expanses of the same general habitat type. In each plot we measured several features of habitat structure and floristic composition and surveyed the bird populations. Here we consider two numerically dominant, widespread species in this system, the Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*).

Territory boundaries of breeding males were mapped at the onset of the breeding season at each site using the consecutive flush technique (Wiens 1969); mappings were corroborated and adjusted (where necessary) using subsequent behavioral observations. Males of both species occupy exclusive, nonoverlapping singing territories, although areas

The Auk 102: 500–505. July 1985

TABLE 1. Mean sizes (ha) of breeding territories of Sage and Brewer's sparrows on plots at four shrubsteppe locations. Dashes indicate that the species was absent from a plot.

			Sage Sparrow		Brewer's Sparrow	
Site	Plot	Year	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)
ALE	1	1976	9	0.65 (0.10)	—	—
		1977	10	0.72 (0.19)	—	—
	2	1976	6	1.57 (0.16)	—	—
		1977	3	1.53 (0.20)	—	—
Cabin Lake	1	1976	2	2.09 (0.40)	9	0.86 (0.23)
		1977	6	1.78 (0.49)	8	0.97 (0.35)
		1978	2	3.49 (0.23)	8	0.83 (0.14)
		1979	2	3.88 (0.09)	13	0.67 (0.23)
		1980	3	2.12 (0.14)	8	0.88 (0.16)
		1981	5	1.29 (0.24)	10	0.55 (0.15)
		1982	2	1.72 (0.08)	8	0.63 (0.06)
		1983	2	1.57 (0.20)	9	0.67 (0.14)
	3	1976	2	2.27 (0.21)	8	0.87 (0.13)
		1977	4	2.39 (0.67)	9	0.97 (0.12)
		1978	2	2.77 (0.72)	5	0.91 (0.14)
		1979	4	1.82 (0.53)	8	0.83 (0.35)
		1980	2	2.20 (0.54)	6	0.95 (0.20)
		1981	4	1.29 (0.28)	6	0.64 (0.14)
		1982	3	1.88 (0.21)	6	0.95 (0.26)
		1983	5	1.64 (0.22)	5	1.17 (0.19)
Fort Rock	1	1981	3	1.66 (0.36)	6	0.90 (0.24)
		1982	3	1.76 (0.15)	4	1.25 (0.28)
		1983	4	1.76 (0.38)	6	0.72 (0.14)
	2	1981	4	1.88 (0.26)	5	0.95 (0.31)
		1982	5	0.99 (0.17)	5	1.01 (0.29)
		1983	3	1.86 (0.38)	9	0.75 (0.11)
Star Creek	1	1976	2	3.08 (1.08)	—	—
		1977	3	2.40 (0.42)	1	2.36
		1978	5	1.76 (0.12)	—	—
	2	1976	1	5.49	—	—
		1977	1	5.79	10	0.86 (0.17)
		1978	1	5.81	11	0.82 (0.12)

used for foraging may overlap. Territory sizes were determined by use of an area-conversion grid. Estimates of breeding population densities of the species on each plot were determined by counting the number of territories and proportions of territories occurring within the plot boundaries and multiplying this value by 2.0, as males of both species mated monogamously and all birds were paired. Our measure of density is thus reasonably independent of territory size, as it is based on the *number* of territories occurring within a specified area rather than on the sizes of individually mapped territories *per se*.

RESULTS

Sage Sparrows generally occupied larger territories than did Brewer's Sparrows, but territory sizes for both species varied substantially among the sites, plots, and years we sampled (Table 1). We used analysis of variance (ANOVA) procedures to determine whether or not there was any pattern to this variation. Because the two species were distributed differently over the sites and plots (Table 1), however, the data could not be grouped for analysis in the same way for both species. For Sage Sparrows, we first examined territory-size variations over the plots sampled at ALE, Cabin Lake, and Star Creek in 1976 and 1977. This analysis restricted the temporal scope of the comparison but maximized the geographical spread considered. Over this range of samples, variation in territory size was significant (ANOVA, $F = 11.83$, $P < 0.001$), and site, plot, and year all contributed significantly to this variation (Table 2). Territories at ALE averaged significantly smaller than those at Cabin Lake, which in turn were

TABLE 2. F values and df for three-way ANOVA showing effects on territory size of site, plot nested within site, year, and the year by nested plot interaction for Sage and Brewer's sparrows.

	Sage Sparrow[a]		Brewer's Sparrow[b]	
	df	F[c]	df	F[c]
Site	2	33.68***	1	5.57*
Plot (site)	2	6.32**	1	0.48
Year	1	17.74***	1	0.62
Year × plot (site)	4	3.10*	2	0.89

[a] Tested for plots at ALE, Cabin Lake, and Star Creek in 1976 and 1977.

[b] Tested for plots at Cabin Lake and Star Creek in 1977 and 1978.

[c] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

smaller than territories at Star Creek (Tukey's studentized range test; $P < 0.05$). This pattern was consistent between years, although in 1977 territories at Star Creek were slightly smaller than at one of the Cabin Lake plots. Although the strength of the year effect differed among plots, 1976 territories were larger than 1977 territories at all locations except one plot at ALE, where territory sizes were similar in both years.

A more restricted geographical comparison can be made of Sage Sparrow territories at the Cabin Lake and Fort Rock plots over the period 1981-1983. Territory sizes varied significantly over this series of samples (ANOVA, $F = 3.49$, $P < 0.003$), but none of the main effects (site, plot, year) contributed significantly to this variation; only the year-plot interaction was significant (Table 3). Separate between-site, between-plot, and between-year tests failed to reveal any significant differences. Finally, in a comparison of plots at the Cabin Lake site over

TABLE 3. F values and df for three-way ANOVA showing effects on territory size of site, plot nested within site, year, and the year by nested plot interaction for Sage and Brewer's sparrows. Both species were tested for years 1981-1983 at the Cabin Lake and Fort Rock plots.

	Sage Sparrow		Brewer's Sparrow	
	df	F[a]	df	F[a]
Site	1	0.81	1	7.48**
Plot (site)	2	0.74	2	19.02***
Year	2	1.22	2	4.41*
Year × plot (site)	6	5.03**	6	4.92***

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 4. F values and df for two-way ANOVA showing effects on territory size of plot and year and plot by year interaction for Sage and Brewer's sparrows. Both species were tested for years 1976-1983 at the Cabin Lake plots.

	Sage Sparrow		Brewer's Sparrow	
	df	F[a]	df	F[a]
Plot	1	2.04	1	22.81***
Year	7	14.14***	7	5.71***
Year × plot	7	7.43***	7	2.84**

[a] ** $P < 0.01$, *** $P < 0.001$.

the period 1976-1983 (Table 4), there was significant overall variation in territory size (ANOVA, $F = 8.91$, $P < 0.001$), almost all of which was attributable to between-year rather than between-plot differences. Territory sizes on the plots varied similarly with year except for a divergence in 1979 (Fig. 1), which accounts for the significant plot-year interaction term (Table 4).

For Brewer's Sparrows, the broadest geographical comparison (between plots at Cabin Lake and Star Creek in 1977 and 1978) revealed no significant overall pattern of variation in territory size (ANOVA, $F = 1.83$, $P = 0.13$; Table 2), although territories at Cabin Lake averaged significantly larger ($P < 0.05$) than those at Star Creek. A comparison of plots at the Cabin Lake and Fort Rock sites during 1981-1983 indicated significant overall variation (ANOVA, $F = 7.14$, $P < 0.001$; Table 3), with effects of site, plot, and year all contributing significantly to the variation. The plots at each site varied in a similar manner, with territory size increasing over the 3 yr at Cabin Lake, and increasing between 1981 and 1982 and then decreasing in 1983 at Fort Rock. If we consider just the Cabin Lake plots over the 1976-1983 period, overall variation in territory size was significant (ANOVA, $F = 5.16$, $P < 0.001$; Table 4), with both plot effects and year effects of major importance. Territories in plot 2 were always larger than those in plot 1, and the variation between years was in the same direction for both plots. The magnitude of the year effect, however, differed between plots (Fig. 1), especially during 1981-1983.

These analyses indicate that a good deal of the variation in territory sizes shown in Table 1 is statistically significant and involves differences between sites, between plots at sites, and

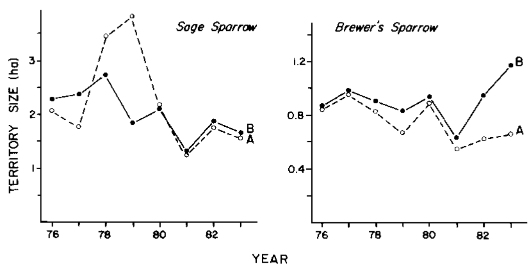

Fig. 1. Mean territory sizes of Sage and Brewer's sparrows on two plots at the Cabin Lake site, 1976–1983. A = plot 1, B = plot 3.

between years. The fact that at least some of the variation in territory sizes is consistent suggests that it may be related to variation in underlying environmental features or in population densities. We could not use ANOVA procedures to explore the relationships between variation in territory sizes of each species and habitat features or population densities, but we could conduct correlation tests over the entire series of sites, plots, and years sampled in our studies.

Territory sizes of Brewer's Sparrows did not vary systematically in relation to any of the habitat features we measured (Table 5), even though there were substantial habitat differences between sites, plots, and years. On the other hand, territory size of Sage Sparrows was positively related to coverage of spinescent shrub species (e.g. *Atriplex* and *Tetradymia* spp.) and to an index of vegetational horizontal heterogeneity or patchiness, while varying inversely with total vegetation coverage and its horizontal variation and with coverage of grass (bunchgrasses) and sagebrush. Thus, over this range of sites and habitats in the northwestern shrubsteppe, Sage Sparrow territories generally were smaller in areas with more grass and sagebrush and larger in the more heterogeneous areas dominated by spinescent shrubs (chiefly at the Star Creek site).

These associations are in general opposite to those relating Sage Sparrow population densities to habitat variables (Wiens et al. MS), suggesting that there may be an inverse relationship between density and territory size. There are, of course, other reasons to expect such a relationship—in many species, territory size decreases as the density of birds occupying a local plot increases until some minimal size or degree of compressibility is reached, as visu-

TABLE 5. Correlations between sizes of breeding territories of Sage and Brewer's sparrows and several habitat variables, derived over the entire range of sites, plots, and years sampled. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ( ) = $0.10 > P > 0.05$; NS = not significant.

Variable	Sage Sparrow	Brewer's Sparrow
n	25	17
Coverage[a]		
Total vegetation	−0.45*	NS
Grass		
Total	−0.52**	NS
Bunchgrass	−0.55**	NS
Shrub		
Total	NS	NS
Sagebrush	−0.58**	NS
Spinescent shrubs	0.88***	NS
Rabbitbrush	NS	NS
Standing dead	(−0.33)	NS
Hits[b]		
0–30	(−0.37)	NS
30–60	NS	NS
>60	NS	NS
Maximum interval[c]	NS	NS
Diversity[d]		
Shrub species	NS	NS
Physiognomic	NS	NS
Heterogeneity index[e]	0.46*	NS
Litter[f]		
Total cover	NS	NS
CV cover	−0.41*	NS

[a] Recorded as the proportion of vertical point samples at which vegetation type was present.

[b] Number of contacts of vegetation of any type in 30-cm height increments of a point sample passed vertically through the vegetation.

[c] Highest 10-cm increment of the vertical pin recording vegetation contacts.

[d] Measured using Hill's (1973) formula, $D = 1/\Sigma p_i^2$, where p_i = proportion of the *i*th shrub species or physiognomic vegetation type in the sample.

[e] A measure of horizontal patchiness in vegetation distribution (see Wiens 1974, Rotenberry and Wiens 1980).

[f] Plant detritus on the ground; coverage measured as for vegetation. CV = coefficient of variation of litter depth between sample points.

alized in Huxley's (1934) "elastic disk" conceptualization. Perhaps, then, the variations in territory sizes for either or both species are related to breeding population densities.

To assess this relationship, we subjected the density and territory-size data to regression analysis. Mean territory size decreased with in-

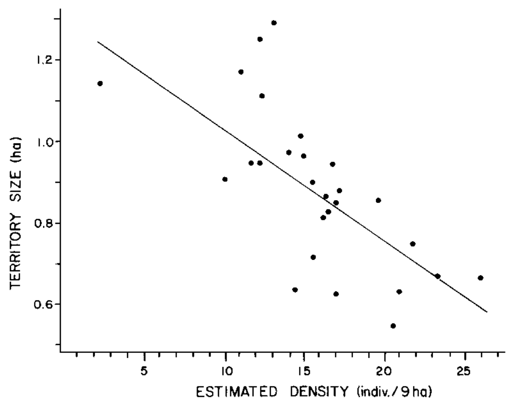

Fig. 2. The relationship between mean territory sizes of Brewer's Sparrows over the series of sites, plots, and years sampled and estimated breeding densities on those sample areas. The line indicates the linear regression. Values from an additional plot at Cabin Lake were included in this analysis to increase sample size, and thus the number of points shown exceeds the number of entries in Table 1.

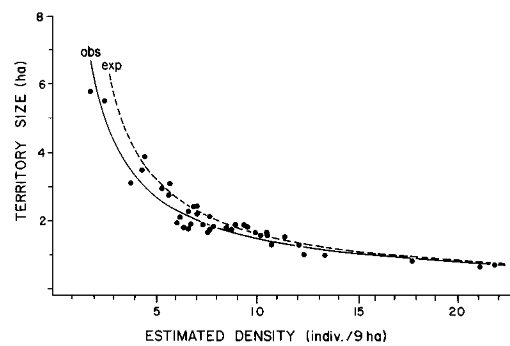

Fig. 3. The relationship between mean territory sizes of Sage Sparrows over the series of sites, plots, and years sampled and estimated breeding densities on those sample areas. The "obs" line indicates a power function fitted to the data; the "exp" line indicates the relationship expected from a null model of space occupancy assuming full saturation of area (see text). Values from additional plots at ALE and Cabin Lake were used in this analysis, and thus the number of points exceeds the number of entries in Table 1.

creasing population density in both species, although in different manners. For Brewer's Sparrows the best regression fit was obtained from a linear model (Fig. 2; $y = 1.30 - 0.0025x$, $r^2 = 0.52$, $P < 0.001$; exclusion of the one outlying value from the analysis did not alter the fit appreciably). Sage Sparrow territory sizes, on the other hand, showed a strong curvilinear response to changes in population density (Fig. 3); a power function provided the best fit to the data ($y = 88.2x^{-0.87}$; $r^2 = 0.92$, $P < 0.001$).

DISCUSSION

These patterns suggest that, over the range of habitat conditions and densities that we sampled, Brewer's Sparrows steadily contract their territories as population density increases. There is some indication that territory sizes may reach an upper limit at moderate densities (perhaps 100 individuals/km^2) and do not expand further at lower densities (e.g. 25 individuals/km^2, Fig. 2), despite the availability of large expanses of unoccupied habitat bordering the territories. For this species, however, our data provide no evidence of a lower limit of territory compressibility, even at high densities at which plots are completely covered by breeding territories. In Sage Sparrows, on the other hand, territories rapidly expand in size at low densities, with no apparent upper limit. At intermediate to high densities, however, territory size hardly changes with increasing density, suggesting that a minimal acceptable size has been reached (Fig. 3).

Huxley's (1934) "elastic disk" idea leads one to expect that when minimal territory size is attained, available habitat is fully saturated and further increases in population density will not be permitted; this is the logic behind the proposition that territory can act to regulate population size (Brown 1964, von Haartman 1971). If suitable habitat within plots is not saturated, however, population density may continue to increase beyond the point at which territory size reaches a minimum (which presumably is determined by individual behavior and habitat-use patterns rather than by interindividual interactions) through annexation of unoccupied areas. It was apparent from our field maps that study plots often were not fully saturated with breeding territories—gaps existed between territories in habitat that was not measurably different from that in unoccupied areas. As one way of examining the pattern of territory-size variation in Sage Sparrows in relation to plot saturation, we compared the observed territory-size/density pattern with that generated from a premise of total plot occupancy at all densities. Thus, for example, if a 10-ha plot were completely occupied and contained only two territories, one would expect each to be 5 ha in size; if 10 males held territories on the plot, each would occupy a territory of 1 ha, and so on. The curve generated on this basis is shown in Fig. 3. At intermediate to high density, it matches the observed regression quite closely, suggesting that the plot was indeed fully saturated at those densities. At lower densities, however, observed territory sizes were usually less than those predicted from this model, substantiating the direct field evidence that the plots were not completely saturated.

These results have implications for studies that attempt to document patterns of habitat selection. When density in an area is low, available habitat may not be fully saturated, and individuals may be free to exercise "optimal" habitat selection (Fretwell and Lucas 1969, Wiens 1973). As the area becomes more fully saturated at higher densities, however, the habitat options available to individuals for territory location become increasingly restricted, forcing occupancy of "suboptimal" conditions and blurring patterns of habitat preference. As a consequence, the habitat occupancy patterns that are expressed in plots that differ in their degree of saturation will differ, in at least a partially density-dependent fashion. This complicates attempts to infer patterns of habitat occupancy or preference from plot-based surveys.

What can we conclude from these analyses? In the absence of information on resource levels, we cannot attach clear ecological meaning to the variations in territory size that occur in both species, although territory size-density relationships clearly are different in the two species. Territory sizes *do* vary, however, from location to location within the shrubsteppe, from plot to plot at the same location, and from year to year in the same plot. This variation is sometimes substantial, and at least some of it is associated with changes in local population densities and, for Sage Sparrows, with features of the habitat as well. These findings suggest that "average" values of territory size for a species should be viewed with some caution, and that closer examination of the details of territory-size variations within species in relation to population and environmental features may be a fertile area for investigation.

Acknowledgments

Our research has been supported by the National Science Foundation, most recently by grants DEB-8017445 and BSR-8307583. Bob Pietruszka, Luke George, and Gary Miller commented on an initial draft of this paper; they and Roy Mason, John Steele, Linda Heald, Steve Zack, Rich Bradley, Marsha Lewis, Neil Cobb, and Janet Kjelmyr assisted us in the field. Gary Miller contributed to the development of the null model in Fig. 3.

Literature Cited

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160-169.

Carpenter, F. L., & R. E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194: 639-642.

Fretwell, S. D., & H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoret. 19: 16-36.

Gill, F. B., & L. L. Wolf. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56: 333-345.

von Haartman, L. 1971. Population dynamics. Pp. 391-459 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427-432.

Huxley, J. S. 1934. A natural experiment on the territorial instinct. Brit. Birds 27: 270-277.

Peters, R. H. 1983. The ecological implications of body size. Cambridge, England, Cambridge Univ. Press.

Rotenberry, J. T., & J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228-1250.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8: 1-93.

———. 1973. Interterritorial habitat variation in Grasshopper and Savannah sparrows. Ecology 54: 877-884.

———. 1974. Habitat heterogeneity and avian community structure in North American grasslands. Amer. Midl. Natur. 91: 195-213.

———. 1984. Resource systems, populations, and communities. Pp. 397-436 *in* A new ecology: novel approaches to interactive systems (P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, Eds.). New York, John Wiley & Sons.

———, & J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51: 21-41.