The Condor 92:264–266

COMPARISONS OF THE BEHAVIOR OF SAGE AND BREWER'S SPARROWS IN SHRUBSTEPPE HABITATS[1]

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Key words: Sage Sparrow; Brewer's Sparrow; Oregon; shrubsteppe; behavior; habitat use; Amphispiza belli; Spizella breweri.

Sage Sparrows (*Amphispiza belli*) and Brewer's Sparrows (*Spizella breweri*) are the most common breeding birds in vast areas of *Artemisia*-dominated shrubsteppe in western North America. They are frequently locally syntopic, occupy broadly overlapping territories (Wiens et al. 1985, 1986; Petersen and Best 1987), and are ecologically very similar to one another (Wiens and Rotenberry 1981, Wiens et al. 1987a), especially at a local scale.

Given this overall similarity and the relative simplicity of the habitats that the birds occupy, it is appropriate to ask how they do or do not differ in their behavior and habitat use. We have previously documented shifts in the behavior of these species in response to experimental manipulations of habitat structure (Wiens et al. 1986) and variability in their behavior associated with time or location (Wiens et al. 1987b). Here, we compare the two species directly, using observations gathered over several years on two plots at a single location.

METHODS

Our observations were gathered during 1976–1979 at the Cabin Lake site, 70 km southeast of Bend in central Oregon. We established two 9-ha gridded plots in sagebrush/rabbitbrush (*Artemisia tridentata/Chrysothamnus* spp.) shrubsteppe, within which we recorded the behavior of breeding males. Because our emphasis was on the frequency with which specific behaviors occurred rather than on the structure of the total activity budget or the duration or sequencing of these behaviors, we used a form of interval sampling (Altmann 1984, Bakeman and Gottman 1986), noting the activity and substrate of an observed individual at 20-sec intervals. We preselected individuals for observation at the outset of each day's observations so that sampling would be equalized among individuals and over time periods during the day over a 1-week period. Observations were made by quietly following individuals at a distance of 8–15 m; most individuals were observed for 30 min to 1 hr, although in a few instances birds were lost from view after 10–15 min of observation. Observation sequences of <3 min were not used in the analyses. We categorized behavior into five activity types (foraging, flight, inactivity, aggression, and singing) and five substrates (sagebrush, other shrubs, ground, grass, and air). Intervals during which a bird was momentarily out of sight were recorded but were not included in the analyses. Data were gathered by seven observers who were carefully trained in categorizing activities and substrate types. Observers were rotated between plots to avoid any systematic biases. Most observers gathered information over several years.

Because our observations were focused on the behavior and habitat use of locally syntopic populations, repeated observations of the same individuals were necessary in order to obtain adequate samples. This raises the possibilities that the patterns we observed may not be representative of the population as a whole and that multiple observations of the same individuals are not independent samples (Machlis et al. 1985). We minimized these problems by sampling the behavior of all individuals holding territories on the plots. During our studies, 8–11 Sage Sparrows and 12–16 Brewer's Sparrows were observed in each plot during each season.

The details of our analytical procedures are described by Wiens et al. (1987b). Briefly, we used each sequence of interval observations of an individual (an "observation string") as a single sample of activity and substrate-use patterns. For each observation string, the percentage of the 20-sec interval point samples at which a given activity type occurred or substrate type was used was calculated to produce a set of frequency values for activity and substrate types. We then analyzed the variation of each activity or substrate-use category separately. The data were normalized by a combination of log and arcsine transformations and analyzed using a fixed-effects model analysis of variance (ANOVA).

These data sets usually contained some observation strings in which a given activity did not occur or substrate type was not used. Although this had little effect on the analyses for the common activities or substrates, the frequency distributions for the less frequent activities or substrates were dominated by zero values even after transformation. To address this problem, we combined observation strings from short periods of observation of individuals (in which zero values were likely to occur) to create observation strings at least 15 min

[1] Received 18 August 1989. Final acceptance 20 October 1989.

long, from which activity and substrate-use frequencies were then calculated. Observation strings in which a category did not occur even after combination were excluded from the ANOVA tests. In a more general analysis of the behavior of these species (Wiens et al. 1987b) we used *G*-tests to compare behaviors or substrates with large proportions of zero values in observation strings. Because we focus in this paper on the more common activities and substrates and because the results of *G*-tests closely paralleled the ANOVA results, we present only the latter.

In this paper we report the results of the statistical tests rather than the transformed or original data or mean values. Because sample sizes for the different observation categories were not equal, the relative proportions of time spent in each activity or on each substrate did not sum to 1.0, and the distribution of values was strongly skewed, the untransformed mean values would provide little real indication of the similarities or differences between the species and might produce erroneous impressions. Although the data transformations and adjustments justified our statistical procedures, they resulted in numbers that have no intuitive meaning whatsoever; presentation of these values would likewise be misleading.

RESULTS

Our previous analyses (Wiens et al. 1986, 1987b) have shown that both Sage and Brewer's sparrows apportion their activity time and substrate use nonrandomly. Despite such nonrandom behavioral patterning, the appropriate null hypothesis for interspecific comparisons is that the species do not differ. To test this hypothesis, we conducted two analyses, one comparing the activity budgets and substrate-use patterns of the species between years (plots pooled), the other examining between-plot patterns (years pooled). These comparisons generated a large number of ANOVA tests, the results of which are summarized in Table 1.

Brewer's Sparrows spent more time singing than did Sage Sparrows, significantly so in 1978 and 1979. This difference was consistent on both plots. In contrast, no consistent differences between the species in the frequency of foraging behavior were apparent. Brewer's Sparrows foraged more than Sage Sparrows in 1976 (ns) and 1977 ($P < 0.05$), whereas Sage Sparrows foraged more in 1978 (ns) and 1979 ($P < 0.001$). Sage Sparrows were more frequently inactive in all years except 1976, leading to a consistent difference between the species on both plots. Sage Sparrows spent more time in flight in 1977, but the differences did not emerge as consistent over years for either plot. There were no significant between-species differences in the frequency of aggression, either within years or within plots.

The species differed more clearly in their use of substrate types than in activities. Brewer's Sparrows used sagebrush substantially more than Sage Sparrows in all years except 1976 and in both plots, whereas Sage Sparrows made greater use of open ground. This pattern probably reflects the greater amount of singing by Brewer's Sparrows and their clear preference for sagebrush as a substrate for singing (Wiens et al. 1987b).

Between-species differences in the use of other species of shrubs were inconsistent. Brewer's Sparrows spent significantly more time in this substrate in 1976, whereas

TABLE 1. Summary of ANOVA tests of between-species differences in the composition of behavioral repertoires and substrate-use patterns of Sage and Brewer's sparrows at Cabin Lake, 1976–1979. * = $P < 0.05$, ** = $P < 0.1$, *** = $P < 0.001$, ns = $P > 0.05$. Parenthetical terms give the rankings of species for significant terms in the ANOVAs.

Test		Activities					Substrates				
		Singing	Foraging	Inactive	Flight	Aggression	Sagebrush	Other shrubs	Ground	Grass	Air
Within-year	1976	ns	ns	ns	ns	ns	ns	**(B > S)	**(S > B)	ns	ns
	1977	ns	*(B > S)	***(S > B)	*(S > B)	ns	***(B > S)	***(S > B)	***(S > B)	***(S > B)	**(S > B)
	1978	***(B > S)	ns	***(S > B)	ns	ns	*(B > S)	ns	***(S > B)	—	ns
	1979	***(B > S)	***(S > B)	***(S > B)	ns	ns	***(B > S)	ns	***(S > B)	ns	*(S > B)
Within-plot	1	**(B > S)	ns	***(S > B)	ns	ns	***(B > S)	ns	***(S > B)	ns	ns
	2	**(B > S)	ns	***(S > B)	ns	ns	***(B > S)	*(S > B)	***(S > B)	**(S > B)	ns

Sage Sparrows used other shrubs more in 1977. Sage Sparrows used other shrubs significantly more than Brewer's Sparrows in plot 2 (which contained a mixture of sagebrush and rabbitbrush), but not in plot 1 (which was almost entirely sagebrush). Grass was also used significantly more by Sage Sparrows than by Brewer's Sparrows in 1977 and (years combined) in plot 2. Overall, then, between-species differences in substrate use (but not activities) were greater in plot 2 than in plot 1, and yearly differences in substrate use were greatest in 1977, least in 1976 and 1978.

DISCUSSION

These results indicate that, although the two species are generally similar in their behavior, differences do exist, especially in the patterns of substrate use. Our previous analyses of the behavior of these species (Wiens et al. 1987b) have shown that there is considerable yearly, between-plot, and between-site variation in activities and, especially, substrate use. The greater degree of difference between the species in substrate use than in activity (as gauged by the greater number of significant differences shown in Table 1) might reflect this flexibility of substrate use in each species, which would increase the possibility that they might differ. On the other hand, when we experimentally altered habitat structure in a different plot at Cabin Lake (Wiens et al. 1986), both species altered the frequency distributions of their activities in the manipulated area but neither altered its substrate-use patterns. Some of the same differences between the species that we found in the present study (e.g., the tendencies for Brewer's Sparrows to sing more and forage less and to use sagebrush more frequently and open ground less than Sage Sparrows) also emerged when we compared the species in the habitat-manipulation study. When we attempted to relate the patterns of activities and substrate use of each species to environmental features such as population densities, community composition, or coverages of the substrate types, however, few consistent and readily interpretable relationships were evident (Wiens et al. 1987b).

In another study (Rotenberry and Wiens, unpubl.), we compared the attributes of patches of vegetation selected for foraging by Sage and Brewer's sparrows to the same measures of patches that we selected at random from the same area. In a comparison of patch types used by the two species, the only significant difference was in patch size: Brewer's Sparrows selected larger patches. Brewer's Sparrows intersperse periods of singing in their foraging bouts, and, because patch size is highly correlated with patch height, this difference between the species in these foraging-based observations may be a consequence of the prediliction of Brewer's Sparrows to sing from elevated perches.

What can we conclude from these comparisons? The behavior of each species varies between years and between plots, largely independently of that of the other species. This variation, which may reflect a combination of sampling error and individual idiosyncrasies, tends to obscure any but the strongest patterns of relationships to environmental variables or differences between the species. Some patterns that emerge on one plot in some years are absent in other years or on the other plot. Still, the species do differ consistently, primarily in the inclination of Brewer's Sparrows to sing more than Sage Sparrows and (perhaps as a result) to use the dominant elevated perches (sagebrush) more frequently. Brewer's Sparrows sing a lengthy, complex song whereas Sage Sparrow vocalizations are relatively short and stereotyped (Wiens 1982). The species have similar between-bout intervals during the peak of singing (Wiens, unpubl.), so Brewer's Sparrows might be expected to use song-associated substrates more than Sage Sparrows. The differences in behavior and substrate use between the species may therefore be more closely related to differences in their breeding biology than to resource-based ecological separation.

Rich Bradley, Roy Mason, Gary Miller, Bob Pietruszka, and John Steele spent many hours following sparrows and recording observations, and their efforts are much appreciated. The research was conducted on lands administered by the Bureau of Land Management, and was supported by a series of grants from the National Science Foundation. Kenneth Petersen and John Zimmerman offered thoughtful and constructive comments on the manuscript.

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