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A LESSON IN THE LIMITATIONS OF FIELD EXPERIMENTS: SHRUBSTEPPE BIRDS AND HABITAT ALTERATION¹

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Abstract. We manipulated the habitat composition and structure within territories of birds breeding in the *Artemisia*-dominated shrubsteppe of central Oregon in order to assess how closely individuals track habitat in features such as territory placement or size or behavioral budgeting and space use. We removed 75, 50, 25, and 0% of the shrub individuals from 625-m² blocks in a checkerboard design. Over the following 7 yr we monitored territorial locations and sizes and breeding densities of Horned Larks (*Eremophila alpestris*), Sage Sparrows (*Amphispiza belli*), and Brewer's Sparrows (*Spizella breweri*) on the manipulated area and an adjacent unaltered control area. Activity and substrate-use patterns and intensity of use of the different treatment blocks within the manipulated area were also determined for the two sparrow species. Sage Sparrows, which from our previous studies appear to be more closely linked to shrub (sagebrush) coverage than the other species, did not respond to the manipulation at a local population level. The manipulation apparently did affect territory placement and densities of Brewer's Sparrows and Horned Larks in 1980–1982, but these trends were not consistent over the entire postmanipulation period. Densities of all species varied among years. For Brewer's Sparrows and Horned Larks these variations did not parallel those in nearby census locations, but Sage Sparrow densities varied in the same ways over all the locations. These variations appeared to parallel variations in biyear (October–April) precipitation, with a 1-yr time lag. Individuals of both sparrow species altered the details of their activity budgeting, but not their substrate-use patterns, in response to the manipulation. Both species clearly expressed an affinity for unmanipulated blocks within the manipulation area.

This experimental manipulation is complicated by influences of time lags on individual and population responses that may stem in part from site tenacity by breeding adults, leading them to return to previous breeding locations in years following the manipulation despite the habitat changes. Further, the spatial scale on which the manipulation was conducted may have been inappropriate to gauge responses at the population level. We suggest that these complications may plague many field experiments in ecology.

Key words: *Brewer's Sparrow; experiment; habitat selection; Horned Lark; Oregon; Sage Sparrow; shrubsteppe; territoriality.*

INTRODUCTION

The ways in which birds respond to variations in habitats have profound implications for a wide range of topics in ecology and behavior. Foraging patterns may be influenced by the patch structure of a habitat (MacArthur and Pianka 1966), mating systems by habitat structure and productivity (Verner and Willson 1969, Emlen and Oring 1977), species packing in communities by vertical structure (MacArthur and MacArthur 1961, Cody 1968), predation risk by the availability of dense microhabitat (Pulliam and Mills 1977), and so on. All of these relationships are consequences of the process of habitat selection by individuals (Cody 1985, Wiens 1985), which may be influenced by both the structural configuration (e.g.,

Hildén 1965, Wiens 1969) and floristic composition (e.g., Holmes and Robinson 1981, Wiens and Rotenberry 1981) of the habitat.

Most often the detection of patterns of habitat occupancy by bird species is approached by correlating variations in the presence or absence of species or their abundance with variations in habitat features over a series of locations. This is the "natural experiment" approach (Schoener 1974, Diamond 1983), which we have used in most of our investigations of bird-habitat relationships in North American grassland and shrubsteppe ecosystems (Wiens and Dyer 1975, Rotenberry and Wiens 1980*a, b*; Wiens and Rotenberry 1981). It is the most effective way to discern the basic patterns of ecological systems, but it has inherent weaknesses (Clutton-Brock and Harvey 1979, Connell 1980, Diamond 1983, Thornhill and Alcock 1983). In particular, such comparisons can only provide hints about the

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processes underlying the patterns, and often they say little of the dynamics by which the patterns are established or of the responsiveness of *individuals* to habitat changes. Direct experimental manipulations in the field have been suggested as a remedy to this problem under appropriate circumstances (Connell 1980, Newton 1980, Wilbur 1984), and they have become increasingly frequent in ecology (see reviews by Schoener [1983] and Connell [1983]). Such experiments also have inherent weaknesses and limitations, however (Diamond 1983, Bender et al. 1984, Hurlbert 1984), and often these are not recognized until the completion of the experiment (if then). One of our objectives in this paper is to use one field experiment to draw attention to some limitations on such studies that may not always be evident.

Depending on the questions being asked, field experiments may involve manipulation of resources such as food or habitat, or alterations of the species present in the community or their relative abundances (Wiens 1984). Investigators of food limitation of populations or of individual foraging behavior, for example, have generally manipulated resources (Newton 1980), while those studying possible competitive relationships have added or removed species from the community (Connell 1983, Schoener 1983). In investigating avian habitat relationships, species additions or removals are often not feasible, given the mobility of individuals and legal and ethical constraints on collecting. One can, however, alter features of the habitat.

In this paper we report the results of one such experiment, in which we manipulated the structural configuration of shrubsteppe habitats at the scale of individual territories. Because the experiment was conducted on an area including several territories, we could assess the responses of segments of the populations of several bird species as well as responses of individuals to systematic changes in habitat. We specifically addressed the hypotheses that, as a consequence of the habitat manipulation, birds in subsequent years will:

- 1) shift their territories away from the manipulated area, reducing population densities there;
- 2) alter territory sizes so as to maintain a relatively unchanged habitat configuration within the territories;
- 3) alter their activity budget or substrate use in the manipulated area relative to the control area; and/or
- 4) shift their use of space within territories to avoid manipulated zones.

In addition (5), different bird species will respond to the manipulation in different ways, in manners predictable from their habitat correlations over the shrubsteppe region as a whole.

METHODS

Study area and species

The manipulations were conducted at Cabin Lake, in the northwestern Great Basin cold desert shrub-

steppe. The study plot was located 6 km east of the Cabin Lake Guard Station, Deschutes National Forest, Oregon (43°30' N, 121°00' W), at an elevation of 1390 m. Precipitation averages 28.8 cm per year, most (70%) occurring during the October–April “bioyear” (Thorpe and Hinds 1977). The vegetation is dominated by shrubs, primarily sagebrush (*Artemisia tridentata*), with *Chrysothamnus viscidiflorus* and *C. nauseosus* occurring at lower coverages except in recently disturbed sites. Breeding bird communities in this habitat usually contain 3–7 species (Wiens and Rotenberry 1981). Numerically, the avifauna is dominated by Brewer’s (*Spi-zella breweri*) and Sage (*Amphispiza belli*) sparrows, Sage Thrashers (*Oreoscoptes montanus*), and Horned Larks (*Eremophila alpestris*). All of these species except the thrashers occurred on the manipulation area in sufficient numbers to permit analysis of their responses to the manipulation, although only the sparrows were common enough for behavioral observations and analyses.

Habitat manipulation

During the breeding season of 1976 we established a 9-ha study plot, gridded at 50-m intervals. The vegetation (habitat) structure and composition of the plot were measured using the procedures described in Rotenberry and Wiens (1980b) and the habitat variables employed by Wiens and Rotenberry (1981). Another 9-ha plot (Cabin Lake) was established in similar habitat 3 km away, and two 610-m transects were set up the following summer in the same general area; censuses from these unmanipulated areas (see Wiens and Rotenberry [1981] for transect census methods) provided a baseline against which the population density variations on the manipulated area could be compared.

During the winter of 1976–1977, when the birds were absent from the area, we altered the vegetation on half of the manipulation plot, leaving the remaining half as a control. To manipulate the habitat on the scale of patches of vegetation within individual territories, we divided each of the 50 × 50 m grid sections on the manipulation half of the plot into 25 × 25 m blocks, from which we removed 75, 50, 25, and 0% of the shrub individuals present (Fig. 1). In each block, we removed individual shrubs (e.g., every other shrub in the 50% removal block), cutting them at ground level with a brush cutter. The treatment was similar to that used by Parmenter and MacMahon (1983) but affected a larger area and followed a “checkerboard” rather than a total removal design. Such a manipulation is not an easy undertaking; in all, over 340 person-hours were required to complete the systematic shrub removal on the 4.5-ha manipulation area. The plot was surrounded by a vast area of habitat generally similar to that in the control half of the plot. Because the control and manipulation halves of the plot abutted one another, there was a possibility of “edge effects” in which patterns in one half might be affected by those in the other

half. An alternative manipulation design would be to separate the control and manipulation areas by some suitable distance and to surround the manipulated area by a buffer zone of similarly manipulated habitat. This would have been logistically prohibitive, however, and the greater distance between the control and manipulation areas might also have rendered them sensitive to different environmental influences in this patchy environment. We attempted to minimize edge effects by restricting our analysis to observations or samples taken primarily within one or the other half. We did not use observations from territories or individuals occupying both halves of the plot.

The manipulation thus created a "checkerboard" of blocks containing different shrub coverages and shrub spacings. An average-sized Brewer's Sparrow territory (the smallest territory of the three species we considered) might contain a dozen such blocks. The manipulation was expected to produce an overall reduction of 37.5% in shrub coverage on the manipulated half of the plot. Shrub coverage on the control half of the plot in the summer following the manipulation was 22%, that in the manipulated half 15%, a reduction of 31.8%. Sagebrush coverage was reduced from 22 to 14% (36.4%). Grass coverage was unaltered (28 vs. 26%).

Measures of bird responses

To test hypotheses 1 and 2, we mapped individual territories on the entire plot at the onset of each breeding season, in late May or early June, using the flush-map procedure of Wiens (1969). By tabulating the number of territories or portions of territories included within halves of the plot and adjusting for the mating status of each species, population densities could also be estimated (although the small size of the areas renders these estimates somewhat imprecise). Hypotheses 3 and 4 were tested using data gathered from systematic observations of the behavior of individual male Brewer's and Sage sparrows. During the breeding seasons of 1977–1979, we followed individuals on this plot, recording at 20-s intervals their behavior (foraging, nonforaging locomotion [mainly flight or long runs], aggression, singing, and inactive) and the substrate (sagebrush, other shrubs, grass, ground, or air) in which the behavior occurred. Birds readily adjusted to our quiet and unobtrusive observation protocol: individuals were usually followed at 5–15 m, a distance selected because of the absence of evident influences of the observer on activities. At times, individuals that were being followed were out of sight. This was considered as a neutral activity state, and was not included in the analyses. If an individual was out of sight for >1 min, the observations were terminated. Observations were evenly distributed over the day, the breeding season, and the two halves of the plot. The analysis of such behavioral observations is by no means straightforward. Observations taken from a stream of ongoing behavior at 20-s intervals are not statistically indepen-

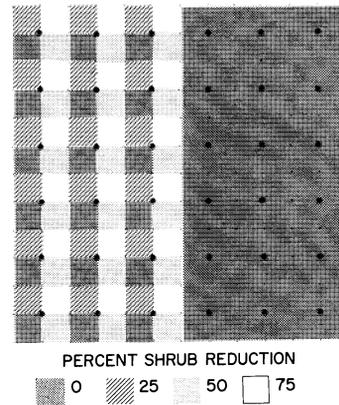


FIG. 1. Design of the experimental habitat manipulation. Dots mark grid points located at 50-m intervals; shrubs were removed from the left half of the plot according to the percentages indicated in the key.

dent samples of behavior. To circumvent this problem, we considered each sequence (or "string") of continuous observations of an individual as a single sample. For each string, the percentage of all observations assignable to each of the activity categories and to each of the substrate categories was calculated. These data were arcsine transformed. In some cases, however, high numbers of zeros skewed the distributions, particularly for rare behaviors and substrates. We omitted these "zero strings," in which a given activity or substrate category did not occur, from the analysis of variance (ANOVA) tests for that activity or substrate. ANOVAs were, therefore, conducted separately for each activity or substrate category, using the transformed percentages for only those observation strings in which the category occurred. We conducted *G* tests parallel to each ANOVA comparison to test the frequency of occurrence of the activities and substrates in all strings ("zero" strings included). In all cases, the results of the *G* tests were consistent with the results of the ANOVAs, and we therefore present only the latter analyses here.

Plots of these percentages of activities and substrate-type uses within observation strings revealed a high variance associated with shorter strings, particularly for rare behaviors. The variance appeared to stabilize at ≈ 45 observations (15 min of continuous observation). In order to minimize the possibility of committing a type II error because of the high variances, we combined short strings (<45 observations) within the categories being compared and recalculated percentages devoted to activity and substrate types within these lumped strings.

For the analysis of treatment-block use on the manipulated half of the plot we used the percentage of each string devoted to use of each of the three manipulation blocks, the control block, and the off-plot area. In the treatment of these data, however, we did not exclude "zero strings," as the manipulation blocks were small enough that most observation strings included

TABLE 1. Average coverage values (%) for several vegetation variables during the periods immediately following the habitat manipulation (1977–1979) and prior to the termination of observations (1981–1983), on study area and Cabin Lake control site.

Habitat variable	Time period	Experimental plot		Cabin Lake plot (unmanipulated)
		Control half	Manipulated half	
Grass	1977–1979	33.0	32.7	25.7
	1981–1983	32.3	40.0	33.0
Total shrub	1977–1979	23.0	18.7	30.7
	1981–1983	27.0	23.0	36.3
Sagebrush (<i>Artemisia</i>)	1977–1979	18.7	15.0	20.0
	1981–1983	20.3	15.0	24.0
Rabbitbrush	1977–1979	4.3	4.3	11.0
	1981–1983	7.3	10.0	13.7
Bare ground	1977–1979	40.0	42.0	33.7
	1981–1983	42.7	42.7	32.0

activities in each block type, and the frequency of zero strings was thus low. The zero strings also provided information on nonuse of blocks that was central to the analysis.

For the comparisons of activities and substrate uses in the control and manipulation halves of the plot, observation strings had to be classified as occurring in one half or the other, even though some birds we observed occurred in both halves of the plot during a string. We arbitrarily classified observation strings in which >75% of the observations occurred in a given half of the plot as characteristic of that half. Strings that were spread more evenly between the halves were excluded from the analysis.

RESULTS

Persistence of manipulation effects

To evaluate the responses of birds to our manipulation, it is necessary to know whether or not the vegetation changes persisted throughout the period of our study (1977–1983). We measured coverage values of habitat features on the plot every year, using a different array of randomly positioned sampling points each year. Sample sizes on the control and manipulation halves of the experimental plot were rather small (18 points), so we have averaged coverage values for the first 3 yr following the manipulation (1977–1979) and for the 3 yr at the end of the study (1981–1983) (Table 1). Inspection of the data for successive years revealed no gradual or systematic changes within each 3-yr time period. To interpret any habitat changes between these time periods, one must also know what habitat changes might be occurring in this shrubsteppe system quite apart from any manipulation effects, so we have included values from the unaltered Cabin Lake plot for comparison.

Grass coverage increased between the time periods on the manipulation portion of the experimental plot, while remaining unchanged on the control half; the difference between the halves thus increased from 0.3 to 7.7%. Grass coverage also increased substantially on the Cabin Lake plot during the same period, however. Total shrub cover increased somewhat on the manipulation area, but shrub cover increased as well on the control area, maintaining a difference of $\approx 4\%$ between the areas. Shrub coverage also increased on the Cabin Lake area, suggesting that this was a system-wide change rather than a recovery from the manipulation per se. Coverages of sagebrush and rabbitbrush,

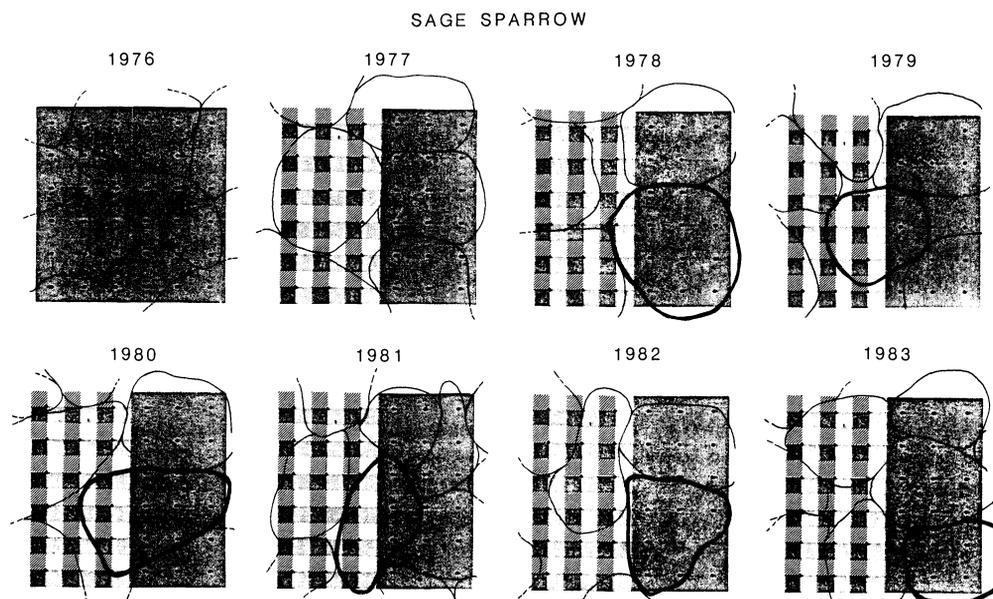


FIG. 2. Territory locations of Sage Sparrows on the experimental plot, 1976–1983. The heavy line denotes the territory of one marked male that occupied the plot over six successive years.

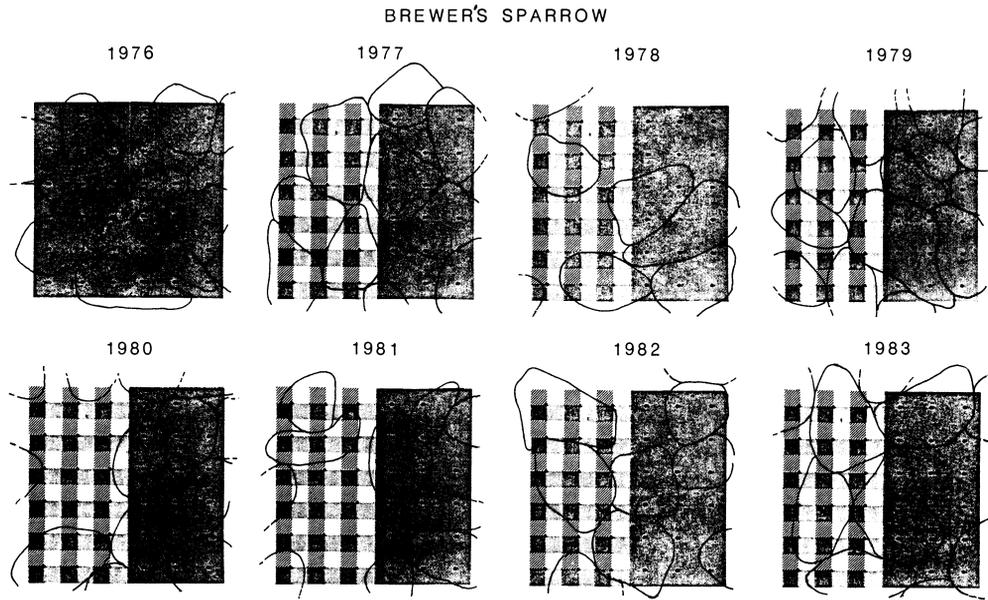


FIG. 3. Territory locations of Brewer's Sparrows on the experimental plot, 1976-1983.

however, changed in different ways. Both increased slightly on the control area and the Cabin Lake plot, but on the manipulation area sagebrush coverage remained unchanged, while rabbitbrush coverage increased more than on the other areas (as might be expected of this disturbance-responsive species). We conclude that the general effects of the habitat manipulation were persistent over the period of our study.

Hypothesis 1: Plot occupancy patterns

The territory mappings demonstrated no obvious avoidance of the manipulation area. Sage Sparrows

occupied both halves of the plot more or less equally in each of the seven years following the manipulation, although in some years (e.g., 1982) their occupancy of the plot was not complete (Fig. 2). Brewer's Sparrows held smaller breeding territories and came close to saturating the plot only in 1976 (the premanipulation year) and 1979 (Fig. 3). In 1980, 1981, and (to a degree) 1982, there were fewer territories of this species in the manipulation area, but this difference did not persist in 1983. Although it is possible that this pattern represented an active avoidance of the manipulated area by individuals during those years, it may also reflect

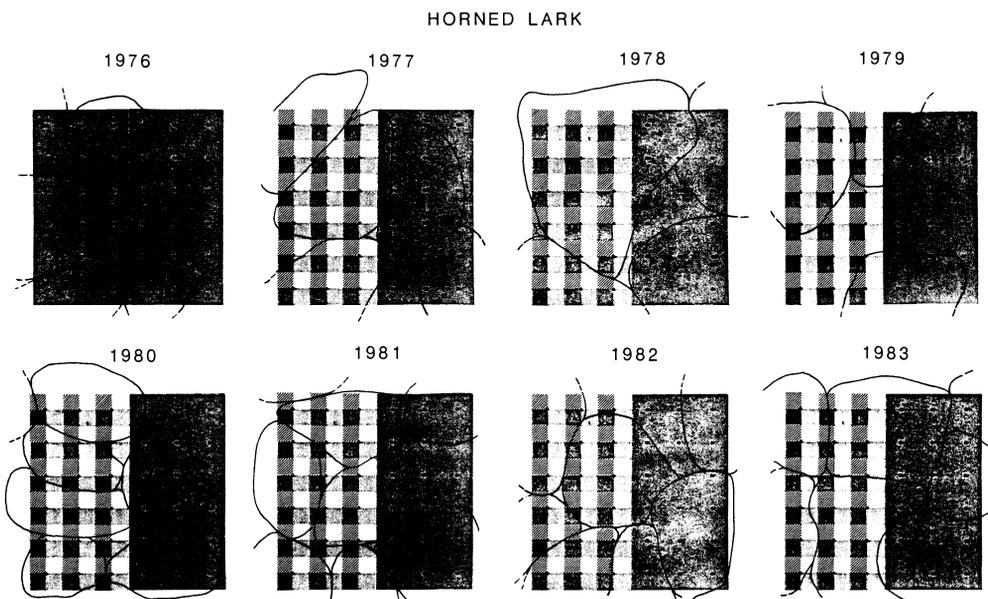


FIG. 4. Territory locations of Horned Larks on the experimental plot, 1976-1983.

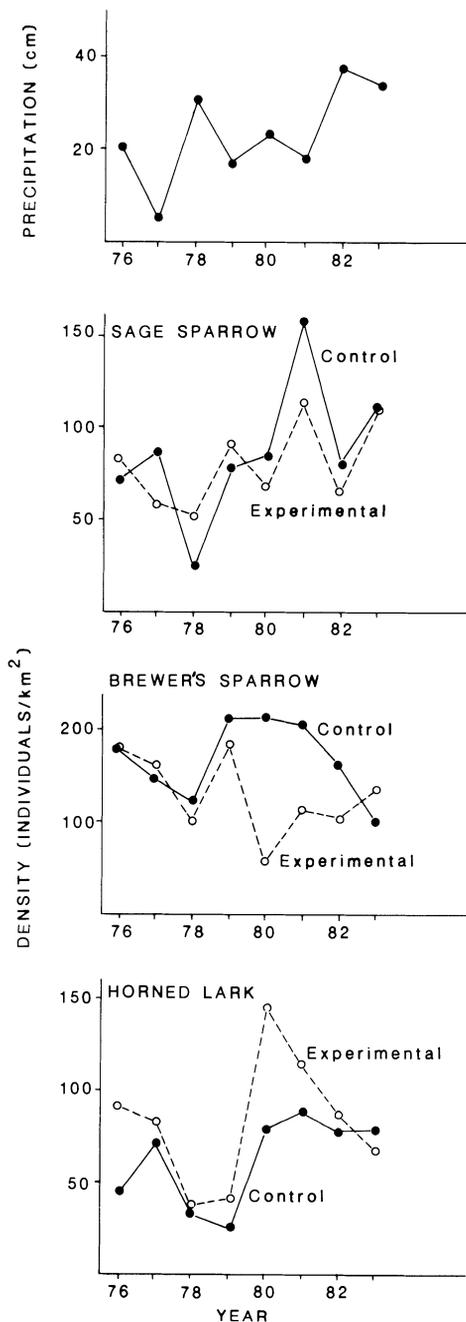


FIG. 5. Estimated breeding densities of the three study species on the control and experimental halves of the manipulation plot, 1976–1983. Shrub density reductions were performed in the winter of 1976–1977. Total biyear (October–April) precipitation at a station 15 km from the plot for the same period is shown in the top panel.

normal spatial variations in territory positioning in an unsaturated habitat. Horned Larks occupied large breeding territories in this shrubsteppe habitat, and thus few of them were contained within our plot. Prior to the manipulation most territories were in the portion of the plot that we subsequently altered, but from 1977

to 1979 there was no clear difference in occupancy patterns of the manipulation and control areas (Fig. 4). More territories were established in the manipulation half of the plot in 1980, 1981, and (to a lesser degree) 1982, but this difference disappeared in 1983. This is the converse of the pattern exhibited by Brewer's Sparrows.

Density estimates derived from the territory mappings portray quantitatively the impressions conveyed visually in Figs. 2–4. Estimated densities of Sage and Brewer's sparrows were similar on the two halves of the plot during the 1976 breeding season, prior to the manipulation, while Horned Lark densities were substantially greater on the area to be manipulated (Fig. 5). Densities of all three species varied on both halves of the plot over the following years; coefficients of variation of annual densities ranged from 27 to 47%, with no systematic differences between species or treatments. Sage Sparrow densities were greater on the control half of the plot in four of seven years, although not normally by very much, and there was no significant overall difference in densities between the manipulated and control areas (Paired t test, $n = 8$, $t = -0.798$, $P = .23$). Brewer's Sparrow densities varied less than those of Sage Sparrows on the control area but were similarly variable on the manipulated area. Densities were greater on the control area in five of seven years, substantially so in 1980–1982 (Fig. 5), and overall were almost significantly greater on the control area ($n = 8$, $t = -1.796$, $P = .058$). Horned Lark densities varied substantially between years, especially on the manipulated area. Densities there exceeded those on the control area in six of seven years, and over all years were significantly greater than on the control area ($n = 8$, $t = 2.393$, $P = .024$). These data suggest a manipulation effect, although the patterns are not consistent over time.

Our ability to discern a clear response to the habitat manipulation in patterns of territory placement or population densities is complicated by the considerable annual variation in densities on both the control and manipulation areas. To assess if this variability was associated with the habitat alterations, we compared the patterns of density variations with those obtained on the Cabin Lake plot and the two census transects. Generally the cvs of annual densities for the species in these census locations were similar to those on the manipulation and control areas, although, as habitats on the census areas differed somewhat from one another and from the experimental area, average estimated densities differed (Table 2). The directions of year-to-year density changes of Sage Sparrows were the same on the control area as in the census locations in almost all years (17 of 19 comparisons; binomial probability $P < .001$), while those on the manipulation area matched trends elsewhere less closely (14 of 19 comparisons), but still significantly ($P < .05$). Density-trend patterns of Brewer's Sparrows, on the other hand, failed to show such consistency over this area: trends on the

TABLE 2. Breeding population density statistics of shrubsteppe birds averaged over years on the manipulated and control halves of the experimental plot and on three nearby census locations.

Plot	No. years	Density (individuals/km ²)								
		Sage Sparrow			Brewer's Sparrow			Horned Lark		
		\bar{X}	<i>s</i>	cv	\bar{X}	<i>s</i>	cv	\bar{X}	<i>s</i>	cv
Experimental plot										
Manipulation	7	80.9	25.4	31.3	122.1	40.9	33.5	82.6	38.7	46.9
Control	7	90.1	39.9	44.3	166.7	45.1	27.1	65.0	25.1	38.6
Cabin Lake plot										
Transect 1	7	108.6	34.6	31.8	215.6	69.9	32.4	39.7	24.0	60.6
Transect 2	7	67.6	13.5	20.0	205.1	52.0	25.3	111.6	31.3	28.1

control area agreed with those elsewhere in only 7 of 19 comparisons and in 10 of 19 on the manipulation area (both $P > .10$). Horned Larks were not present on the Cabin Lake plot, but comparisons of density trends on the halves of the experimental plot with those on the two transect areas failed to reveal much concordance (control: 6 of 12 comparisons; manipulation: 6 of 12 comparisons; both $P > .10$). Densities on the experimental plot thus appeared to be no more variable than those elsewhere in this area, and although Sage Sparrow densities appeared to vary more or less concordantly over the area, those of Brewer's Sparrows and Horned Larks varied independently among census areas a few kilometres apart.

One potential driving variable of this variation is precipitation. In environments such as this shrubsteppe, many facets of system functioning are closely associated with variations in precipitation, especially that occurring during the "bioyear." Bioyear precipitation varied sevenfold during the 8 yr of our study (Fig. 5). Directions of annual bird density changes paralleled the directions of changes in precipitation during the immediately preceding bioyear in only 17 of 56 comparisons. If bird density changes are compared with year-to-year changes in precipitation occurring a year before (i.e., a 1-yr time lag), however, Sage Sparrow density changes parallel rainfall changes in 16 of 18 comparisons ($P < .001$). For Brewer's Sparrows and Horned Larks the extent of concordance is not so great

(13 of 18, $P < .05$; and 7 of 12, $P > .10$, respectively), but is still improved by incorporating a 1-yr time lag. It thus appears that at this site the bird populations may "track" climatic variations, although only rather coarsely. Sage Sparrows seem most closely attuned to variations in precipitation, and this may contribute to their greater consistency in annual density changes over the area as a whole.

Hypothesis 2: Territory size changes

If individuals failed to respond to the removal of shrubs from the manipulation area by shifting territorial locations, they might nonetheless change the size of the area they occupy. If this is so, we would predict that those species with demonstrated affinities for shrubs (Sage Sparrows and, to a lesser extent, Brewer's Sparrows) would increase territory sizes, while those with affinities for more open habitats (Horned Larks) would decrease territory sizes (Wiens and Rotenberry 1981). The few values that are available (Table 3) fail to support either prediction. Territory sizes varied, but in no consistent fashion. Territories of Sage Sparrows were larger on the manipulation area in two of five years, even though mean territory size was generally greater on the control area. Brewer's Sparrow territories were larger on the manipulation area in three of seven years, while Horned Lark territories were smaller on the manipulation area in two of four years.

TABLE 3. Mean territory sizes (ha) of shrubsteppe birds on manipulated and control halves of the experimental plot, 1976–1983. Number in parentheses is sample size. Dashes denote inadequate sample for analysis.

Year	Sage Sparrow		Brewer's Sparrow		Horned Lark	
	Manipulation	Control	Manipulation	Control	Manipulation	Control
1976	0.7 (3)	0.9 (4)	2.0 (1)	2.0 (1)
1977	2.4 (1)	1.9 (2)	1.0 (4)	1.0 (5)	2.1 (2)	1.7 (1)
1978	...	2.8 (2)	0.8 (2)	1.0 (3)
1979	1.5 (2)	2.6 (1)	0.8 (4)	0.7 (3)	2.7 (1)	...
1980	...	2.2 (2)	1.3 (1)	0.9 (5)	1.3 (4)	1.5 (2)
1981	1.4 (1)	1.1 (3)	0.6 (2)	0.7 (4)	1.5 (2)	2.1 (1)
1982	1.8 (1)	1.9 (2)	1.2 (2)	0.8 (4)	2.7 (1)	2.0 (1)
1983	1.6 (2)	1.7 (3)	1.1 (3)	1.3 (2)	2.7 (1)	...
\bar{x} (excluding 1976)	1.7 (7)	1.9 (15)	0.9 (18)	0.9 (26)	1.9 (11)	1.8 (5)

TABLE 4. Activity budgeting of Sage and Brewer's sparrows in control and manipulation halves of the experimental plot. Values are mean proportions of n individual observation strings occupied by a behavior.*

Species	Activity†	Control‡		Manipulation‡		P§
		n	\bar{X}	n	\bar{X}	
Sage Sparrow	Foraging	71	0.35	65	0.40 ^a	.07
	Locomotion	70	0.04 ^a	58	0.06	.03
	Inactive	66	0.12	60	0.19	.003
	Aggression	22	0.03	25	0.05	.81
	Singing	75	0.51	64	0.35 ^b	.0002
Brewer's Sparrow	Foraging	77	0.42	48	0.32 ^a	.03
	Locomotion	56	0.08 ^a	38	0.09	.62
	Inactive	50	0.15	31	0.15	.52
	Aggression	16	0.06	13	0.03	.22
	Singing	72	0.51	45	0.65 ^b	.002

* Data are averaged over all observation strings (series of status checks at 20-s intervals) occurring in the control or manipulation area. Because the analyses use different sets of observation strings for each activity type, proportions sum to >1.0 .

† Behaviors with sample sizes <10 observation strings are not included.

‡ Activities in the same column designated with the same superscript letter differ significantly ($P < .05$) between species.

§ Significance level of difference in behavior between control and manipulation halves of plot; Tukey's studentized range test.

Hypothesis 3: Activity budgeting and substrate use

Individuals might respond to the habitat manipulations by altering their behavior or substrate use in the manipulation area. Overall, both Sage and Brewer's sparrows devoted much of their time to singing and foraging, less time to sitting inactively, and relatively little to long movements or aggressive behaviors. In comparison to their behavior on the unaltered control half of the plot, Sage Sparrows sang significantly less, were significantly less active, and moved more often in the manipulated area (Table 4). In other words, where patches of vegetation were more widely spaced, the birds remained stationary and relatively silent in one location longer and then flew between patches. Sage Sparrows also tended to spend more time foraging on the manipulation half of the plot. Brewer's Sparrows, on the other hand, foraged significantly less in the manipulation than in the control area, but spent significantly more time singing in the manipulation area.

The bulk of the activity of both species occurred in sagebrush, the dominant shrub in both halves of the plot (Table 1). They spent somewhat less time in other shrub species and little time in grass, on the ground, or in the air. Utilization of these substrate types by both Sage and Brewer's sparrows did not differ significantly between control and manipulated areas (Table 5). Thus, although the activity patterns of both species differed between the experimental and control areas, the use of substrate types did not.

Hypothesis 4: Use of manipulated blocks

Both sparrow species clearly used the blocks from which no shrubs had been removed significantly more than the altered blocks (Table 6). Sage Sparrows also

tended to spend less time in the most heavily altered blocks, although this trend was not significant.

Hypothesis 5: Species differences

Over a geographic area spanning the range from tall-grass prairies to shrubsteppe, Sage and Brewer's sparrows exhibit significant affinities for habitats with high shrub coverage, low grass coverage, and substantial vertical development and horizontal patchiness in vegetation distribution. Horned Larks, however, attain greatest densities in areas characterized by generally low vegetation (Rotenberry and Wiens 1980a). Within the shrubsteppe environment, however, different habitat patterns emerge, depending on the scale on which they are viewed (Wiens 1985, 1986). Analysis of data from four locations in Washington, Oregon, and northern Nevada indicates a positive association of Sage Sparrows with greater grass and bare ground coverage but negative correlations with shrub coverage and vegetation patchiness (J. A. Wiens et al., *personal observation*). An analysis based on measures from 14 locations in central and southeastern Oregon shrub deserts, on the other hand, indicates no significant correlations of Sage Sparrow densities with habitat structure, but a positive association with sagebrush coverage (Wiens and Rotenberry 1981). Brewer's Sparrows and Horned Larks exhibit no significant associations with habitat structure on either scale, but vary negatively with the coverage of some spinescent shrub species (*Atriplex* and *Tetradymia* spp.) on the 14-site scale.

Although these habitat occupancy patterns are inconsistent, we might generally anticipate a negative response by Sage and Brewer's sparrows (perhaps less marked in the latter) and a positive response by Horned Larks. Yet Sage Sparrow territory locations and population densities were generally unresponsive to the manipulation. Brewer's Sparrows responded negative-

TABLE 5. Substrate use by Sage and Brewer's sparrows in control and manipulation halves of the experimental plot. Values are mean proportions of *n* individual observation strings during which a substrate type was occupied.*

Species	Substrate†	Control‡		Manipulation‡		<i>P</i> §
		<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	
Sage Sparrow	Sagebrush	75	0.58 ^a	66	0.57 ^a	.85
	Other shrubs	74	0.27 ^b	65	0.20	.11
	Ground	60	0.12 ^c	63	0.12 ^b	.86
	Grass	31	0.03	47	0.04	.07
	Air	71	0.05 ^d	62	0.06	.07
Brewer's Sparrow	Sagebrush	59	0.76 ^a	48	0.74 ^a	.56
	Other shrubs	55	0.18 ^b	46	0.22	.28
	Ground	17	0.03 ^c	12	0.04 ^b	.88
	Grass	1	...	0
	Air	51	0.07 ^d	42	0.07	.70

* Data are averaged over all observation strings (series of status checks at 20-s intervals) occurring in the control or manipulation area. Because the analyses use different sets of observation strings for each substrate type, proportions sum to > 1.0.

† Substrates with sample sizes < 10 observation strings are not included.

‡ Substrates in the same column designated with the same superscript letter differ significantly ($P < .05$) between species.

§ Significance level of difference in substrate use between control and manipulation halves of plot; Tukey's studentized range test.

ly in territory placement and densities on the manipulated area in a least some years. Horned Larks, on the other hand, responded to some degree in an opposite manner, increasing in territory occupancy and densities on the manipulated area. To the extent that responses to the manipulation were apparent, then, they differed among species in the expected directions.

More detailed comparisons may be made of the behaviors of Sage and Brewer's sparrows. The two species were generally remarkably similar in activity patterning (Table 4). Brewer's Sparrows foraged significantly less on the manipulation area than did Sage Sparrows, but tended to forage more on the control half of the plot ($P = .03$). Brewer's Sparrows sang significantly more than Sage Sparrows in the manipulation area, but the proportions of observation strings spent in singing were identical for the two species in the control area. This is apparently associated with the diminished singing by Sage Sparrows and the increased singing activity of Brewer's Sparrows in the manipulation area relative to the control. The two species were otherwise quite similar in activity patterns on the control area, although Brewer's Sparrows did move significantly more than did Sage Sparrows.

The two species differed substantially in their uses of substrates on the halves of the plot (Table 5). Sage Sparrows spent much less time in sagebrush on both the control and manipulation areas, and they used open ground significantly more than Brewer's Sparrows, in both portions of the plot. On the control half, Brewer's Sparrows used other shrub species significantly less and air significantly more than did Sage Sparrows, but in the manipulation area the species did not differ in their use of these substrate types. Thus, despite the lack of any clear differences in substrate use by either species between control and manipulation areas, the two species differed in their use of habitat features. The species

were generally quite similar in their use of treatment blocks within the manipulated half of the plot, although Brewer's Sparrows occupied the 75% removal block significantly more often than Sage Sparrows (Table 6).

DISCUSSION

In our previous, nonexperimental analyses of the habitat occupancy patterns of these shrubsteppe birds (Rotenberry and Wiens 1980a, b, Wiens and Rotenberry 1981), we have argued that the bird communities are not fully saturated with species (see also Wiens 1974, 1977) and that local study plots are not fully packed with breeding individuals. The species seem to occupy these habitats within the shrubsteppe largely independently of the details of habitat structure and of the abundances of other members of this ground-shrub

TABLE 6. Use of treatment blocks in the manipulation half of the experimental plot by Sage and Brewer's sparrows.

Species	Treatment block	\bar{X} *	Significance†
Sage Sparrow (<i>n</i> = 99)	0% removal	0.29	A
	25% removal	0.14	B
	50% removal	0.13	B
	75% removal	0.07 ^a	B
Brewer's Sparrow (<i>n</i> = 78)	0% removal	0.34	A
	25% removal	0.18	B
	50% removal	0.12	B
	75% removal	0.17 ^a	B

* Values are mean proportions of individual observation strings (series of status checks at 20-s intervals) spent in each block type, averaged over all observation strings occurring in the manipulated area. Values do not total 1.00, because some observations, collected off the plot or on the control half of the plot, are not included. Values sharing the same superscript letter in this column differ significantly ($P < .05$) between species.

† Means with different letters in this column are significantly different ($P < .05$; Tukey's studentized range test).

foraging guild. The results of the experimental manipulation are consistent with this interpretation. Clearly, the available habitat is not fully saturated with individuals (Figs. 2–4). At the population level all three species responded in subtle fashions, if at all, to what would appear to be profound changes in habitat structure. Individuals, on the other hand, did alter the details of their activity and substrate and space use in response to the manipulation. Thus, although such habitat alterations do not appear to exert a strong effect on the initial placement of individual territories, they do influence individuals once they have established territorial residence in an area. This suggests that properties of entire territories are not necessarily closely related to features of individual behavior in this system. To determine whether or not these individual behavioral differences in manipulated and unmanipulated areas affect reproductive outputs (fitness) would require detailed information on the breeding success of a large number of individuals and on the survival of their offspring, which we could not obtain. In any case, the manipulation effects on individual behavior are not translated into obvious population-level effects.

At least two factors complicate experimental manipulations such as ours, and these complications may cloud what otherwise might be clearer responses by the birds. First, when field experiments are conducted in ecology, there is often an expectation that responses to the manipulation will be relatively rapid; witness the relatively small proportion of the experimental studies reviewed by Schoener (1983) and Connell (1983) that were carried out over more than a single season or year. In some cases this may reflect a belief that under normal conditions individuals and populations (indeed, communities) track environmental variations rather closely (e.g., Cody 1981). Natural systems are generally characterized by an array of time lags, however (Wiens 1986), and these may act to delay a response to an experimental manipulation or even obviate it altogether.

In particular, site tenacity or philopatry in breeding birds may have profound effects in experiments such as ours. Adults that have previously bred successfully in a specific location may return there in subsequent years, even in the face of habitat changes (Hildén [1965] provides several clear examples). To witness a clear response to a habitat change, one would need to wait until most of these site-tenacious individuals had either died or moved elsewhere. In the meantime, however, they may have produced offspring in the altered habitat that form an affinity for that habitat configuration, through imprinting or similar processes (Hildén 1965, Partridge 1978). We do not have sufficient information to determine whether such a scenario is likely in shrub-steppe birds, but we do know that individuals may exhibit remarkable site fidelity from year to year. One male Sage Sparrow, for example, was banded as a breeding adult on the manipulation plot in 1978 and

returned to occupy a territory in the same portion of the plot in each successive year until we terminated the study in 1983 (Fig. 2). Such behavior can produce substantial time lags in responses to experimental manipulations. Brown et al. (1986) have noted similar effects of long time lags in their experimental manipulations of granivore systems in deserts. Marking individuals to record long-term patterns of philopatry and survival would seem to be an essential component of experimental manipulations involving long-lived organisms. Such time lags also point to the importance of establishing an appropriate premanipulation baseline in field experiments. Our manipulation (like most) was preceded by 1 yr of pretreatment survey, which in retrospect probably was not adequate to judge accurately the dynamics of the system in the absence of perturbation. Use of replicated treatment and control plots would improve one's resolution of responses to manipulations, although at times replication may be quite difficult.

A second complication involves the scale of experimental manipulations. In this study we manipulated an area of 4.5 ha. Although this manipulation required a rather massive effort, it is now apparent that the area may have been insufficient to reveal responses at the population level. Relatively few individual territories of Sage Sparrows or Horned Larks were included in either the manipulation or control portions of the plot. Densities are thus estimated from a small portion of the true population, and site fidelity on the part of a few individuals may have a major effect on territorial responses. Further, because the habitat is not completely saturated with individuals, small-scale redistributions of individuals from one year to the next may produce density changes that are more apparent than real (Rotenberry and Wiens 1980a, Wiens 1981). Although the scale of our experimental habitat manipulations was appropriate to influence the behavior of individuals within their territories, it was probably insufficient to reveal population-level responses.

This observation is sobering, for there is relatively little evidence that ecologists conducting field experiments have very often given careful consideration to selecting the appropriate scale for their experiments. The scale at which investigations are conducted, however, clearly influences the patterns that emerge (Wiens 1981, 1984, 1986, Dayton and Tegner 1984, Wiens et al. 1986). In our case, a scale of a few hectares is probably appropriate to address questions relating to how *individuals* relate to habitat or use space, but to ask the same questions at a population scale would probably require an area of at least several square kilometres. Under most circumstances, manipulations on such a scale would be logistically difficult or infeasible. This should not lead to a disregard for the effects of scale in designing and implementing field experiments. Ecologists should take advantage of the opportunities provided by large-scale management manipulations such

as rangeland herbicide treatments (Wiens 1985, Wiens and Rotenberry, *in press*) or clearcutting of forests (e.g., Van Horne 1981) in their design of field experiments.

Two messages of our manipulation experiment are clear. First, breeding birds in this shrubsteppe system do not exhibit strong responses to major changes in the configuration of habitat within their territories, although they do alter their space-use patterns and may modify some features of their activity budgets. There is little evidence of a close tracking of habitat variation when habitat is experimentally perturbed. Second, conducting rigorous field experiments in ecology may be a much more complicated business than many have believed. Experiments must be conducted on a scale that is commensurate with the scale of the patterns or processes being investigated, and often this is not really known. Further, responses to experimental treatments are likely to be obscured by a variety of time lags related to features of the biology of the system. Perhaps one of the unanticipated benefits of such experiments can be the documentation of these time lags and their effects.

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