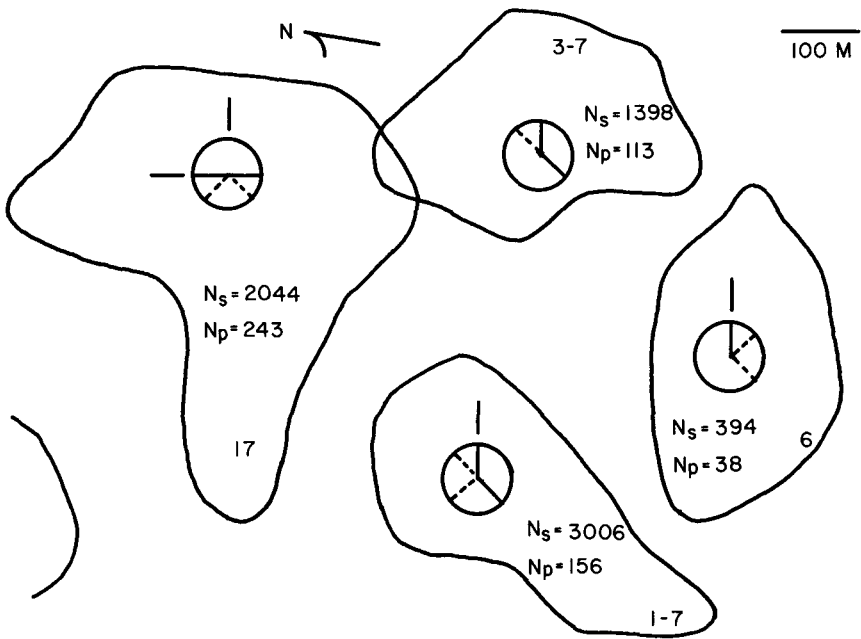


FIG. 1. Orientation of males on song perches in 1976. Solid lines indicate directions of more songs and perches than expected by chance. Dashed lines indicate directions of fewer and no line indicates values near expected (see Methods). Lines inside the circle in each territory are the orientation of songs while the outer lines give orientation of perches.  $N_s$  is the number of songs and  $N_p$  the number of perches used in the analysis for each male.

singing male (direction he was facing) were recorded. Orientation of each male on each perch was classified into 1 of 8 compass directions. I analyzed 2 types of orientation. First, I counted the total number of songs sung in each of the 8 directions for the entire study period (song orientation). Second, I counted only the orientation of the male regardless of how many songs were sung (perch orientation). Thus, for perch orientation, if a male faced direction 1 (east) and sang 100, 20 or 1 song each case would be equal, i.e., each is scored 1 perch in direction 1. If the male changed orientation during a given song bout the appropriate proportions of songs and perches were assigned to each direction. Song and perch orientation for each male was analyzed by a Chi-square goodness-of-fit test to an expected even distribution. In those instances where the Chi-square value exceeded  $\chi^2$ ,  $P = 0.05$ ,  $df = 7$ , I examined subgroups of directions to define those that contributed most to the total Chi-square value. In Figs. 1 and 2, lines indicate directions which contributed most to the Chi-square value; solid lines note directions with greater than expected frequencies and dashed lines, less. No lines indicate the subgroups which did not differ from the expected even distribution at  $P \leq 0.05$ . A complete description of this technique is given in Snedecor and Cochran (1967).

I used the distribution of song perches to calculate 2 centers of each territory following the methods of Post (1974). First, the coordinates of each song perch were weighted by the number of songs at that point (song center). Second, no weighting factor was used (perch center). Territory size was determined by connecting outer perches with straight lines.

An annulus of perch concentration was determined from the number of perches in each



### Orientation - 1977

FIG. 2. Orientation of males on song perches in 1977. Symbols are explained in Fig. 1.

successive annulus of 25-m width. Following adjustment for the increasing area of each annulus the distribution was compared to that expected in a uniform distribution by Chi-square goodness-of-fit.

I then wanted to determine how much of the territory of each male could be adequately described by random movements of the territorial male. The data in Table 1 were obtained by counting the number of perches in each  $25 \times 25$  m plot (subdivisions of the  $50 \times 50$  m grid intervals) in each territory with a value of 0 assigned only if the plot were bordered on 3 sides by plots with at least 1 perch. Other plots with no perches were not considered part of the territory. Then plots with large numbers of perches were successively removed until the remaining distribution of frequencies was not significantly different from the Poisson distribution at  $P \leq 0.05$ .

A 1-way analysis of variance was applied to the data on songs per bout in Fig. 6. Since a significant F ratio resulted, the Student-Newman-Keuls multiple range test was applied to slopes of the log-transformed data. All statistical techniques were taken from Zar (1974).

The vegetation was sampled according to Daubenmire (1959). Two parallel transects were established 50 m apart through each of the 4 territories in 1976. Percentage cover was recorded for each plant species at every 1.5-m interval for a total of 40 points per transect. Vocalizations were recorded with a Dan Gibson Electronic Parabolic Microphone and Uher 4000 Report L recorder. Sound spectrograms were prepared on a Kay Electric Company Sona-Graph, model 6061-B.

TABLE 1  
DISTRIBUTION OF SONG PERCHES PER 25 × 25 M PLOT IN THE TERRITORIES OF MALE  
SAGE SPARROWS

Male	N <sup>a</sup>	Total <sup>b</sup>	$\bar{x}$	S <sup>2</sup> / $\bar{x}$	Random <sup>c</sup>	$\bar{x}$	S <sup>2</sup> / $\bar{x}$	% <sup>d</sup>	N <sup>e</sup>
1-6	237	0-35	9.12	14.55	0-10	2.89	0.89	69	53
2	278	0-18	5.67	4.81	0-8	2.97	2.08	73	111
3-6	322	0-23	5.61	4.46	0-6	2.77	1.14	70	123
4	309	0-13	3.96	3.39	0-7	2.45	1.18	82	158
1-7	189	0-16	3.05	4.90	0-8	2.40	1.63	91	96
3-7	146	0-15	1.95	3.21	0-6	1.57	1.12	96	104
17	300	0-15	3.55	2.89	0-8	2.61	1.32	92	229

<sup>a</sup> Total perches in the territory.

<sup>b</sup> Range of frequency of occurrence of songs per plot.

<sup>c</sup> Range of only those frequencies which yield a goodness-of-fit to the Poisson distribution.

<sup>d</sup> Percent of the 25 × 25 m plots in the territory described by random perch locations.

<sup>e</sup> Perches remaining in the random distribution.

## RESULTS

*Habitat.*—As for most species, structural parameters of habitat influence Sage Sparrow foraging sites, choice of song perches, height of perches and orientation of singing. Habitat may, therefore, have an important effect on the spatial territory. Sagebrush (*Artemisia tridentata*), the dominant species, varied from 11-44% cover, depending on the transect, and the most abundant grass (*Poa sandbergii*) from 4-15% cover. Two other grasses, *Sitanion hystrix* and *Agropyron spicatum* varied from 3-11% cover. *Phlox longifolia* covered from 1-5% of the study area. Only the percent cover of sage varied appreciably, but in a gradual and uniform manner. The habitat appeared homogeneous.

*Territory establishment.*—Sage Sparrows seem atypical among passerines because 7 of 8 males arrived already paired (see Hilden 1965). Arrival dates were 18 March 1976 and 16 March 1977. Males sang little or not at all at first. Initially, pairs mostly foraged together as their territories were delineated. Males 3 and 6 established territories in the same area in both years. In 1977, male 1 established a territory somewhat west of his 1976 territory. The 1977 territory was in the area to which he moved later in 1976 after failing to mate in that year. Identities of males were verified by comparing spectrograms of their songs from both years.

*Territory size.*—Territories varied considerably in size and shape both daily and seasonally with the progress of breeding. Similar variation has been reported for other species (Yarrow 1970, Robins 1971, Yamagishi 1971, Catchpole 1972, Potter 1972, Welsh 1975). Mean territory size for 8 male Sage Sparrows was 4.43 ha ± 1.86 (range 1.06-7.06 ha) and is

larger than the known size for other North American sparrows (see Potter 1972, Rich 1977).

*General behavior.*—Behavior of all males in the morning consisted of single bouts of song from tops of sage, interspersed with foraging. Males seemingly moved randomly through the sage flying up to sing from nearby perches. Typically, a male sang, dropped abruptly and directly to the ground, foraged for some time and then flew directly up to a new perch. Males only rarely foraged above surface in sage or other vegetation. This pattern seemingly reflects the relationship of territorial behavior, foraging, habitat configuration and probably food distribution.

*Territorial behavior.*—Song was the outstanding feature of territorial behavior. There was almost no fighting or visual displaying, a pattern observed in other sparrows (Cartwright et al. 1937, Robins 1971, Potter 1972), and little chasing. I rarely saw physical responses between males. I saw virtually no sentinel behavior in Sage Sparrows. However, such behavior has been reported for Savannah Sparrows (*Passerculus sandwichensis*) (Welsh 1975), Twites (*Acanthis flavirostris*) (Marler and Munding 1975) and Black Rosy Finches (*Leucosticte atrata*) (pers. obs.).

Perched males typically sang at 8–10 sec intervals. One song bout per perch was the rule as perches were always changed immediately after the bout had ceased, and the next bout began within seconds of landing on a new perch. Rarely did males sing while foraging, and then only at intervals of 30–90 sec. Males did not have favorite song perches though they had preferred areas. Some species prefer certain perches (Potter 1972, Catchpole 1972, Welsh 1975), whereas Bewick's Wren (*Thryomanes bewickii*) (Gorton 1977) also shows no preference.

*Song variation.*—Each male uttered a single song type which rarely varied throughout the breeding season except by omission of 1 or 2 of the final syllables. This stereotypy of the primary song has also been observed in other sparrows (Walkinshaw 1939, Borror and Reese 1954, Borror 1959, Goldman 1973, Heckenlively 1976). Males 1, 3 and 6 did not change their songs even slightly between 1976 and 1977 as verified by spectrograms. Martin (1977) reported that some Fox Sparrows (*Passerella iliaca*) also sing identical songs from year to year. Fig. 3 presents songs of 6 male Sage Sparrows.

*Conspicuousness of singing males.*—Males on perches were visible from the front but often difficult to locate from behind. The white breast plumage contrasted with the color of sage, whereas dorsal plumage was cryptically colored. The low pitch of the song combined with abrupt beginnings and endings of most syllables and their short duration maximized locatability of the singer (Thorpe 1956). When singing a male elevated his bill and turned his head from side-to-side throughout each song. All of the

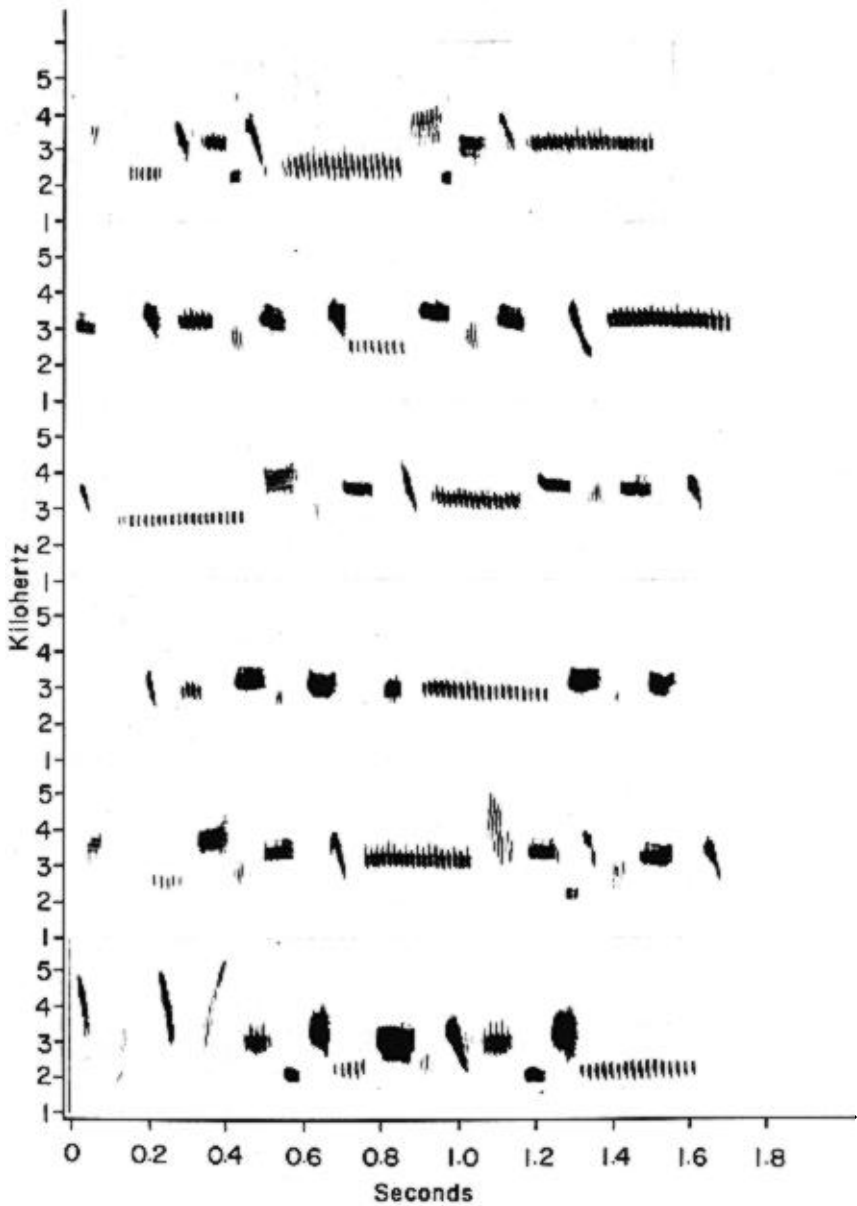


FIG. 3. Sound spectrograms of 6 territorial male Sage Sparrows' songs, (males 1, 2, 3, 4, 17, and 6).

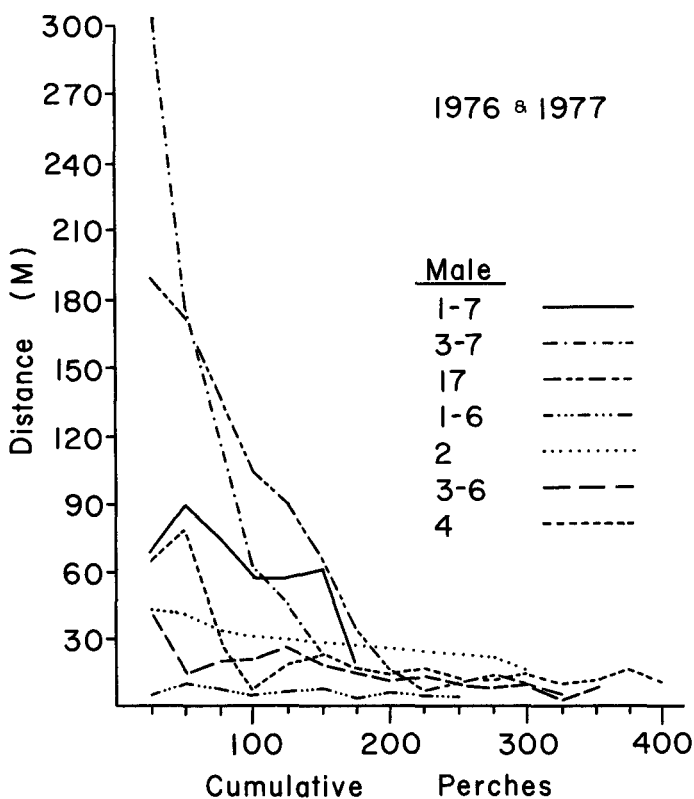


FIG. 4. Distance between the song center of the territories and the perch center after the accumulation of every 25 perches (see text).

above factors facilitated rapid location of singing males when they were facing the observer. Thus, orientation of the male is an important aspect of territorial behavior.

*Song orientation.*—Males did not show evenly distributed song orientation in 1976 (Fig. 1). Males 1-6 and 2 tended to face east and away from neighboring males. Males 3-6 and 4 sang towards each other and male 4 also sang towards male 6. In 1977 (Fig. 2), there was also a preference for certain directions. Males 1-7, 3-7 and 6 sang facing east and unoccupied habitat. Male 1-7's easterly orientation was also towards male 3-7, though a wide buffer zone separated their territories. Only rarely could I hear the 1 male while in the other's territory. Male 17 faced north, a patch of unoccupied habitat and male 3-7. Male 3-7 also faced male 6.

*Perch orientation.*—Perch orientation of the males seemed more ran-

dom than song orientation (Figs. 1 and 2). Males 3-6 and 3-7 had even orientation. Males 1-6, 1-7, 4 and 6 had uneven orientation due mainly to an excess or deficiency of perches in only 1 direction. Males 1-6, 1-7, 2, 6 and 17 all faced east and unoccupied habitat. Male 17 also faced north and unoccupied habitat. Male 4 had fewer perches facing northwest and a neighboring male.

*Center of territory.*—Fig. 4 presents the distance between the perch center and song center of the territories after the accumulation of every 25 song perches. The 2 centers nearly coincided when points for the entire period were considered. For example, for male 4 the distance between the 2 centers was about 80 m after 50 perches and only 10 m after 400 perches. The exception to this trend occurred for male 1-6 where the distance was 4 m after 25 perches and only slightly less than 4 m after 250 perches. This constant displacement revealed that male 1-6 sang more songs on those perches on the side of his territory nearest the rising sun. Both song and perch orientation were also towards the east. Perhaps the stimulus of the rising sun influenced the strong eastward orientation of this male.

*Distribution of perches.*—The variance to mean ratio of perch frequencies (Table 1) revealed that perches were clustered in the territories of each male except male 6 for which there were insufficient data. After the few plots with large numbers of perches were removed from the analysis (see Methods) the remaining distribution of perching frequency was not statistically different from the Poisson distribution and was, therefore, random. The importance of this difference in the distribution of perches (depending on the way the data are treated) is that plots where perches were distributed randomly made up the largest portion of each male's territory. Thus, perches were randomly distributed over 69% of the territory of male 1-6 and 96% of the territory of male 3-7. Percentages for other males fell between these 2 values.

*Annulus of song concentration.*—Males 1-6 and 4 had most of their songs in the center of their territories (Fig. 5). Male 1-6 and 9.4 times the number expected in the center while male 4 had 4.4 times that expected. Males 1-7, 2 and 3-6 sang most in the third annulus, male 3-7 in the fourth annulus and male 17 in the fifth. The median of song concentration was the third annulus while the median of territory radius was the twelfth.

*Songs per bout.*—The males sang between 1 and 118 songs per bout. The mean number of songs per bout varied from 4.76–18.08. The frequency distribution of songs per bout revealed a preponderance of 1-song bouts and a decline in the number of bouts with more songs. I analyzed only the frequency of observations of bouts between 1 and 20 songs, which provided a continuous distribution for all males. Fig. 6 gives the cumulative distribution and slopes of the lines obtained from the log-transformed

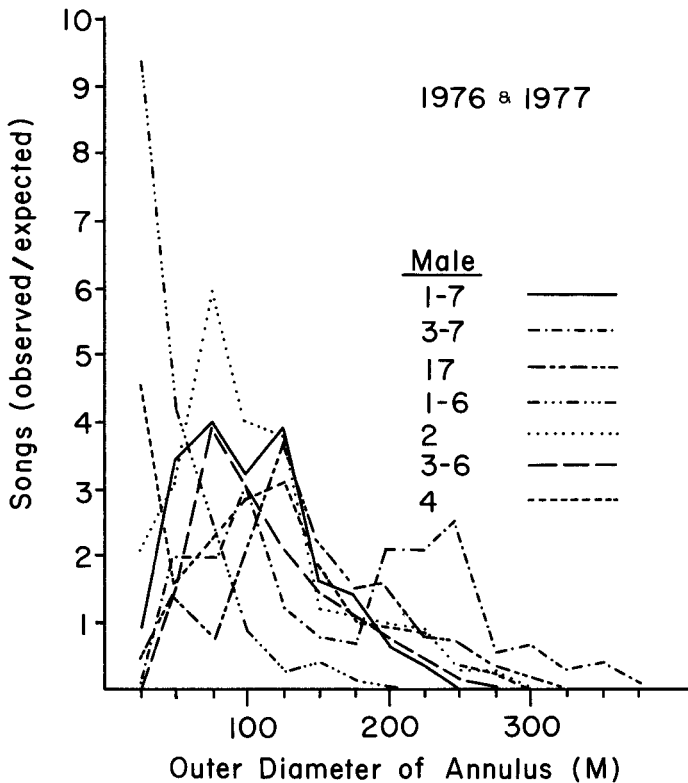


FIG. 5. Distribution of songs in each 25-m annulus from the center of the territories.

data. There are 3 things to notice in this figure. First, the slope of each line is the probability that a male will leave the perch after singing a given number of songs. Second, that probability was similar for all males, ranging from 0.18–0.28. The probabilities were not significantly different for either male 1 or male 3 in both years. Third, the probability was approximately constant for each male. Thus, the probability of leaving the perch after singing the first song was about the same as that of leaving the perch after singing the nineteenth song.

#### DISCUSSION

*Habitat.*—In many territorial species irregularities of habitat provide limiting points (e.g., attractive perch sites, obstructions) for males as they move about the territory singing and foraging (Cartwright et al. 1937, Potter 1972, Welsh 1975). This influence was particularly pronounced in Sa-



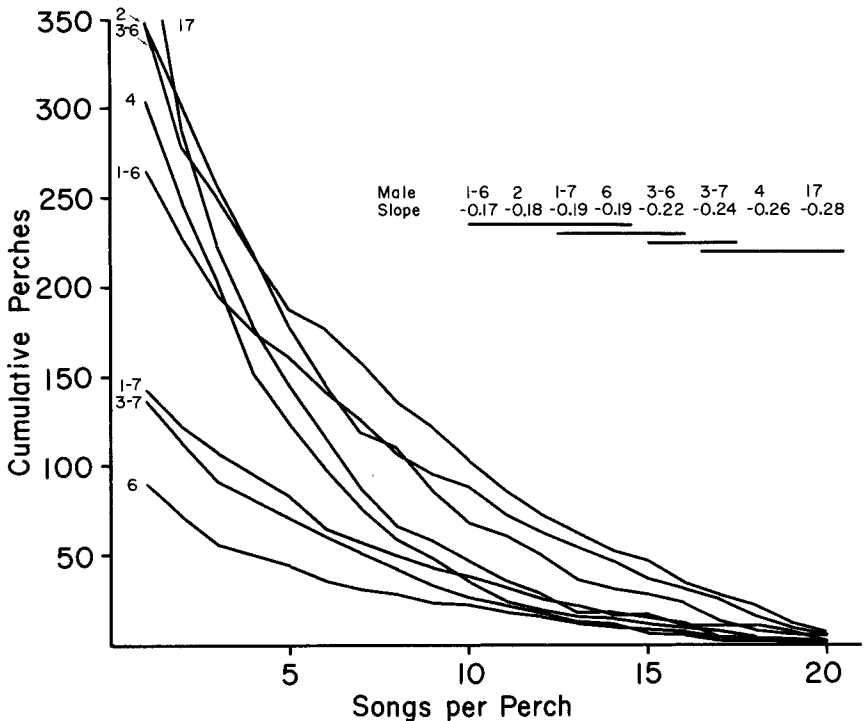


FIG. 6. Relationship between songs per bout and cumulative bouts for each male. Subsets of equivalent slopes derived from the log-transformed data are given.

vannah Sparrows who used fence posts as perches and barbed wire fences as territorial boundaries (Potter 1972). The habitat of the Sage Sparrow varied gradually and, I believe, placed virtually no restrictions on where the males may have moved and perched. The males were free to respond to other factors in the distribution of perches.

*Orientation.*—There were 3 important aspects of orientation. First, males 3-6, 3-7, 4 and 17 sang facing neighbors, but for all males there were several possible directions facing neighbors that did not show excessive singing. Furthermore, males 1-6, 1-7, 2 and 17 sang appreciably fewer songs facing some neighbors. This could be taken to support the idea that males know their neighbors (Weeden and Falls 1959, Falls 1969, Emlen 1971, Wiley and Wiley 1977) and are not sufficiently stimulated to expend energy advertising in their directions.

Verner (1977) predicted from his super-territory hypothesis that the space between territories should be defended if those spaces were large

enough to support a breeding pair. The orientation of males 1-7, 2, 3-6 and 4 towards gaps between territories and the orientation of all 8 males towards unoccupied habitat suggests the latter possibility. Orientation away from neighbors might also serve to reduce the stress between males. Nesting Adeline Penguins (*Pygoscelis adeliae*) orient to inter-nest spaces rather than towards each other (Spurr 1975). But where neighboring Sage Sparrow territories overlapped males oriented towards each other—males 3-6 and 4 towards each other and male 17 towards male 3-7. Also, male 4 faced male 6 in 1976. Male 6 arrived late and persistently sang near the boundary of male 4's territory.

Second, when only perch orientation is considered, none of the directions of excess orientation were towards other males. In fact, 5 of 8 males perched facing east and all males except 3-6 had either song orientation, perch orientation or both to the east. There are at least 3 possible explanations for orientation to the east that may relate to the rising sun. (1) Males may enhance reflection of light from light-colored breast feathers. This may maximize conspicuousness as to reinforce their physical location in the habitat. Conspicuousness would also increase the chances for each male to evaluate the local population size and/or density for which there are apparently minimum requirements in some territorial species (see Hilden 1965:61). (2) The sun may provide early morning warmth. If this were the only consideration it seems that the darker colored back would absorb more radiant energy. Also, males did not fluff feathers as if to conserve heat. (3) Males may orient towards the sun simply because it is the most outstanding stimulus in the environment. The validity of these suggestions could be addressed by observing orientation before sunset and on cloudy days.

Finally, there was a large difference between the number of noted song directions and perch directions. All males showed greater evenness of perch orientation than of song orientation. Recalling the alternating sequences of foraging and singing, it appears as if males flew up to a perch at nearly random directions. Once on a perch the number of songs depended largely on what the bird happened to be facing. This suggests that, except for an orientation towards the sun, males were not reacting to a specific external stimulus when they flew up to a perch. This focuses attention on gross environmental stimuli and internal mechanisms controlling timing and orientation patterns in males. This control of the orientation is further clarified by male 1-6. This unmated male was the only bird showing substantially more or fewer songs in 7 of 8 directions. He sang almost all of his songs in direction 6, 7 or 8 and very few songs in the other 5 directions. His orientation was more predictable and may represent the basic pattern of male orientation that becomes modified upon mating.

*Center of territory and probability of singing another song.*—As more points were added in the calculation of the song center the more closely the song center approached the perch center, as expected in a random system of an infinite number of points. This suggests that for at least 6 of the males the song bout lengths were randomly distributed among the perch locations. The frequency distribution of songs per bout showed that the longer the bout the less likely it was to occur. However, once a distribution of bouts was defined, the spatial distribution of bouts could probably not be predicted. This removes importance from the number of songs in a bout and places more significance with the simple existence of a bout.

The similarity of the distribution of songs per bout for all males and the constant probability of singing 1 more song implies that song bout length is largely under the control of internal mechanisms. A similar distribution was found for calls per bout in Black-capped Chickadees (*Parus atricapillus*) (Ficken et al. 1978). If males sang particular numbers of songs in response to particular stimuli I would expect the frequencies to cluster at 1 or more values. Or if they simply sang until something interrupted them the distribution should have been random.

*Annulus of perch concentration.*—Post (1974) found that there was a difference in the distribution of activity points from the territory centers in Seaside Sparrows (*Ammospiza maritima*) having ungrouped as opposed to grouped territories and was able to ascribe possible selective significance to the observation. Weeden (1965) found that Tree Sparrows (*Spi-zella arborea*) concentrated their activity in the center of the territory with outer zones of progressively diminishing use. Smith (1963) stated that Grasshopper Sparrows' (*Ammodramus savannarum*) song perches were clustered on the periphery of territories as were those of 2 vireos (*Vireo* spp.) (Barlow and Rice 1977). Bonelli's Warbler (*Phylloscopus bonelli*) follows a circuit around its territory which varies little (Bremond 1976). Yamagishi (1971) reported that male Meadow Buntings (*Emberiza cioides*) have 2 centers of activity—one near the nest and another between the nest and the center of the territory. Sage Sparrows have a few plots where many perches are clustered between the edge and center of the territory and closer to the latter. But the remaining perches were scattered randomly throughout the largest part of the territory. Without knowledge of nest locations it is difficult to be certain that the data have been interpreted to best advantage. But when these 2 patterns, random placement and concentration annulus, are observed together, they may represent an optimal placement of songs to convey all the information—species, sex, location, individual identity, motivation—the song of the Sage Sparrow must serve (Marler 1956). Identification of such basic patterns of behavior fa-

elucidate recognition and interpretation of variations which occur in Sage Sparrows in different habitat or of other species in similar habitat.

#### SUMMARY

The distribution of song perches over territories, songs per bout and compass orientation of males on song perches were studied for 8 male Sage Sparrows. Each male had 1 nearly invariable song whose physical characteristics facilitated location of the singer. The uniformly varying habitat did not restrict the males' foraging and perching sites. For 6 males, song bouts of various lengths were distributed randomly among perch locations. Song perches were also randomly distributed in most of the male's territory, although a few 25 × 25 m plots had clustered perches. There was a constant probability that a male would sing 1 more song during any bout. All males showed perch orientation, song orientation or both towards the east and rising sun. Males also tended to sing towards unoccupied habitat and away from neighbors except where they approached too closely or consistently. Gross environmental stimuli, the uniform habitat and internal mechanisms may be important influences on the patterns considered.

#### ACKNOWLEDGMENTS

I am grateful to the Frank M. Chapman Memorial Fund of the American Museum of Natural History for support in 1976 and 1977 and to the Society of Sigma Xi for support in 1977. The Department of Biology, Idaho State University provided equipment and supplies. Charles H. Trost was an endless source of stimulation. William Saul, Edson Fichter, Jack Griffith and Barry Keller helped at various points during the research. I thank Mike Mahoney, Tim Reynolds, Jim McIver and Jim Perry for ideas on various aspects of the work. A special thanks goes to my wife, Pat, for her patience and understanding.

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