TERRITORIAL BEHAVIOR OF THE TREE SPARROW

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Recently Carpenter (1958) has stressed that territoriality should be viewed as a behavioral phenomenon (for example, see Andrew, 1956; Ficken, 1962) rather than a spatial or geographic one. On the other hand, Pitelka (1959) states that territory is primarily an ecological phenomenon, important in partitioning the available habitat. It seems that a quantitative approach to the study of the spatial relations of the territory should provide us with new insight into its functions. Further, measuring spatial relations should give us some indications of the expression of the behavioral systems involved in territoriality.

Previous studies (for example, Kendeigh, 1941; Kluyver and Tinbergen, 1953; Southern and Morley, 1950) have implied that territory size and boundaries are fixed for individual males throughout a season. A few studies have shown that there is a progressive change in territory size as the breeding season advances (Young, 1951; Hochbaum, 1944; Odum and Kuenzler, 1955), but the authors of these studies also gathered their data over an indeterminate and indefinite time interval, not recognizing the strict temporal limitations imposed on territory size. A study of the Ovenbird (*Seiurus aurocapillus*) by Stenger and Falls (1959) showed that this species does not have a static territory with fixed boundaries throughout the season or even for part of the breeding season but rather that the territory consists of a fluctuating, although well-defined, area of utilization that changes from day-to-day or even from hour-to-hour. The changes in the area utilized daily by male Ovenbirds were not random but fell into a pattern that was similar for many individuals of that species. Precisely how this pattern was superimposed upon the changing breeding activities was not clearly understood. The existence of a pattern of change in area utilized by Ovenbirds was an incentive for initiating a study of the changing spatial relations of territorial behavior throughout the breeding season for Tree Sparrows (*Spizella arborea*).

The spatial relations of territory can be subdivided into two categories, both of which were examined in this study. First, comparisons were made between the total activity spaces of individuals in the same study area in one year and between individuals in different years when different population densities prevailed. Banded birds gave some indication of the effect of age on total activity spaces. Second, the dynamic aspects of territorial behavior were examined. These dynamic changes are of two sorts—(1) change in territorial activity during a single day, and (2) change in daily activity space throughout the various stages of the breeding cycle from premating to nestling stages.

Territorial behavior has received considerable attention in the past and thus in the literature there exists the usual confusion of terms (or a confusion of phenomena ascribed to the same term, territory). Tinbergen (1939) indicated that spring fighting and spring territories differ from other kinds of fighting and other kinds of territories. He states that spring (that is, sexual) fighting differs from fighting against predators and food competitors and defense of nest and young.

Among Ovenbirds (Stenger and Falls, 1959) there was a marked difference in the behavior of adult males on the territory once the eggs hatched even though boundaries of a territory were still effectively maintained. Thus, perhaps the nestling territory was different in kind from the mating territory, and possibly the authors were dealing with more than one phenomenon. If Tinbergen's suggestion holds, Tree Sparrows should prove to be good subjects for investigation since territorial activity declines rapidly once the eggs have hatched. Males do not defend the nest, and presumably we are dealing with a single phenomenon—that of spring fighting and spring territory.

The term territory has been variously applied to any situation where a number of observation points for a male bird could be enclosed by a solid line regardless of the time interval involved, or the state of the breeding cycle, or the kind of observation involved. If we are to accept the definition of "any defended area" (Noble, 1939:267) for territory, then the latter term should be applied only when observations of defense are included. Probably the defended area is one of the hardest things to measure and can only be determined when a male is called upon to defend his territory frequently over the interval of study. Such a situation rarely exists for Tree Sparrows in nature, except possibly in very dense populations or when many birds are trying to establish territories simultaneously. Further, defense may be of mates, and fights may not necessarily be confined to an area or the borders thereof.

However, it is possible to measure accurately the space used by a male bird in a clearly defined time interval, which is probably more important and useful than an inaccurately measured defended area over an unclearly defined time interval. Therefore I have studied the daily activity space and total activity space. These are geographic units combining all kinds of observations (fighting, feeding, singing, mating, preening) and having arbitrarily limited time intervals as common denominators. How these areas are related to the areas defended daily or throughout the whole season is not known.

The study was carried out at Eagle Creek, Mile 105, Steese Highway, in interior Alaska (65° 25′ N, 145° 32′ W). Here there is continuous daylight throughout the breeding season of the Tree Sparrow, a conspicuous and abundant inhabitant of this environment. The breeding activities of the whole population are well synchronized, there is one brood per year, and the birds are generally monogamous. Nests are on the ground and easy to find, making it possible to determine accurately the stage of the breeding cycle of each bird.

The study area is covered by subarctic tundra. The vegetation covering the area can be divided arbitrarily into three main vegetational forms—open tundra, low brush, and tall brush. Open tundra, as defined here, consists of plants less than six inches tall. The predominant vegetation comprises lichens, sedges, grasses, dwarf willows, mosses, and numerous forbs. The low brush consists mainly of *Betula glandulosa, Salix* spp. and *Vaccinium uliginosum* growing from six inches to four feet in height and forming a dense and impenetrable mat little used by the Tree Sparrows except along its edges or as song posts. The third type consists of *Salix* spp. and *Alnus crispa* taller than four feet. This type occasionally has an herbaceous understory in which the Tree Sparrows find food and cover. The taller plants also provide numerous song posts. In addition, in a few localities on the study plot, there are isolated spruce trees (*Picea* spp.). These are from 10 to 40 feet tall and may occur in any one of the three vegetation types. They are used as song posts by the Tree Sparrows as well as by several other species.

METHODS

This study necessitated intensive and repeated observations of a few birds in a small area. In each year of the project 9 to 11 pairs were studied, making a total of 30 pairs of Tree Sparrows that were studied over the three years. Since some of the birds returned to the area for more than one year, the actual number of individuals studied was 24 males and 25 females. Most of the birds were color banded, especially those studied in 1960 and 1961. In 1962 we encountered some difficulty in banding the males. Color banding was primarily useful in identifying females and males from one year to the next. For practical purposes, the males could be easily identified by their songs since the song of an individual remains constant and varies, frequently quite considerably, from that of every other male.

The study area was surveyed into a grid, each grid square being 66 × 66 feet (1/10 acre). The grid corners were marked with coordinate letters and numbers on metal tags. In 1960, 25 acres were surveyed in this manner, and in 1961, 40 acres were surveyed. The location of a bird was plotted accurately on gridded paper.

One observer spent an entire observation period of four hours with a single pair of birds, plotting every location visited, every chase, and every activity on a map. The observations were numbered consecutively so that Odum and Kuenzler's (1955) technique could be applied. In this technique, cumulative area is plotted after each five observations. Theoretically an asymptote is reached by the observation-area curve when further observations give no appreciable increase in area. From this asymptotic curve a standard value for area can be arbitrarily chosen, as Odum and Kuenzler did at the point of one per cent change on the curve. These authors did not standardize the time of day at which their observations were made, but we found this to be necessary for the data on Tree Sparrows.

In 1961 and 1962, a standard observation period lasting four hours was established arbitrarily at the same time of day throughout the season. In 1961 the observation period lasted from 3:00 to 7:00 a.m. In 1962 one observer plotted territories from 3:00 to 7:00 a.m. while the other for convenience worked from 2:00 to 6:00 a.m. The shift of one hour did not affect appreciably the size of activity space obtained.

Total activity spaces for both male and female Tree Sparrows were obtained by combining on a single map all locations visited during all observation periods from the building to the nestling stages. The number of observation periods included in these total activity spaces included four to eight four-hour periods in 1960 and 1961 and three to five in 1962. The smaller number of observations in 1962 was due to the fact that I was not on the study area during the early part of the building stage. Also there was a high loss of nests during incubation and early nestling stages. The average number of observations included in each total activity

space was 308 (147–482). On these composite maps all the outside points were connected by straight lines to give a polygon of maximum size. Observations during premating and courting were omitted because occasionally there was considerable shifting of activity spaces of males prior to the arrival and settling of the females.

Daily activity spaces for males were obtained in a similar manner by joining all outside points by straight lines for each four-hour observation period. There were not enough observations for females during any one observation period to give an indication of daily activity space.

The observation-area curve could not be used for estimating areas as will be shown later, but it did give valuable information on the diurnal cycle of territorial activity.

To show degree of utilization of different portions of the total activity space the number of observations in each grid square were counted. The grid squares were then designated as showing intense, moderate, or slight utilization by arbitrarily establishing numerical limits for each of the three degrees of utilization. These limits were set as follows; five or less observations indicated slight utilization, six to 15 indicated moderate utilization, and 16 or more indicated intense utilization. These criteria were established for total activity spaces which included seven and eight observation periods, but since some total activity spaces included less than this number of observation periods, the numerical limits were multiplied by $\frac{X}{7}$, where X represents the number of observation periods included in the total activity space. The degree of utilization of each grid square could then be shown by symbols on a map. Maps were drawn for data of 1961 and 1962 (figs. 1 and 2), although the calculations were made for 1960 as well.

RESULTS

Total activity space of Tree Sparrows.—Male Tree Sparrows either did not maintain rigid boundaries or the location of the boundary could not be established by observing fights between males. Fights among males were not confined to boundaries but frequently covered an area many times larger than the area in which the other daily activities took place. Many of the fights involved more than two birds, usually three and occasionally four birds. The third and fourth birds present usually did not sing. I have assumed that these birds were females. On several occasions this observation was verified by the presence of banded females. On the other hand, males often intruded into another male's activity space when there were no females involved and no fights ensued. Thus it seems that much of the fighting that took place among Tree Sparrows was over females rather than over an area of ground. This confirms the earlier suggestion that activity spaces are more realistically measured than defended areas.

Inspection of total activity spaces (figs. 1 and 2) suggested the existence of a core of concentrated use with an outer cortex where visits were sparse. The nature of this core area was often regularly polygonal. Sometimes, however, the shape of the core was decidedly lopsided or highly irregular. Occasionally the core was divided into two fractions by an area of slight or moderate utilization (for example, males 24 and 19 in fig. 2, or male 10 in fig. 1). Generally the cortex extends more or less equally all around the core so that the core is centrally located within the total activity space. In a few cases, however, the core is eccentric (for example, males 8, 16, and 10 in fig. 1, and males 23 and 17 in fig. 2). Comparison of figures
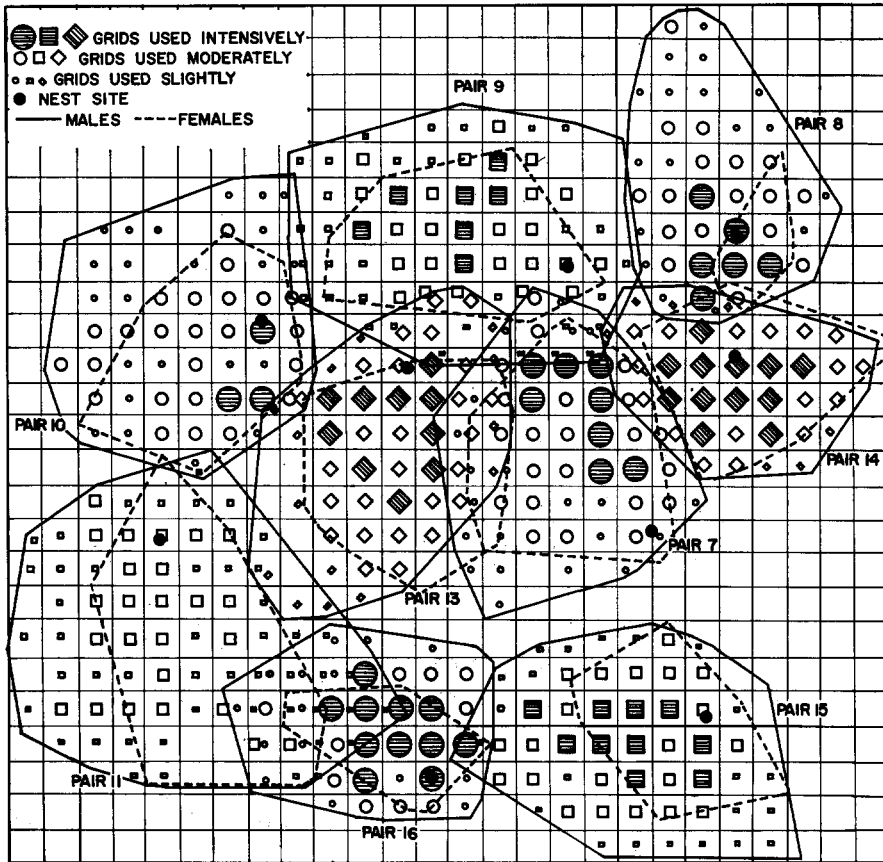
Fig. 1. Location and utilization of total activity spaces of males, location of total activity spaces of females, and location of nest sites of Tree Sparrows on the study area in 1961.

1 and 2 shows that in 1961 when total activity spaces were generally larger the cortex was relatively much greater in extent than in 1962.

The utilization data is summarized in figure 3 and suggests some noticeable differences related to differences in the size of the total activity space. A theoretical model of total activity space can be established by considering the total activity space a series of three concentric circles, the innermost of which includes within it the core of intense utilization, the next one outward includes the area of moderate and intense utilization, while the outer one includes the entire activity space. The models were established by calculating the radii of the circles having the mean areas of the intensely, moderately, and slightly used portions of the total activity spaces. For the two years 1960 and 1961, although there is considerable difference in mean area of total activity spaces, there is not so much difference in the radii. Thus, the general picture for utilization is similar in these two years (fig. 3). In 1962, total activity spaces were smaller with a considerable reduction in radius of the theoretical model. The innermost circle of most intense utilization is greater than in the two preceding years and is relatively greater than the portion used moderately and slightly. Thus, as total activity space becomes compressed the outer cortex becomes
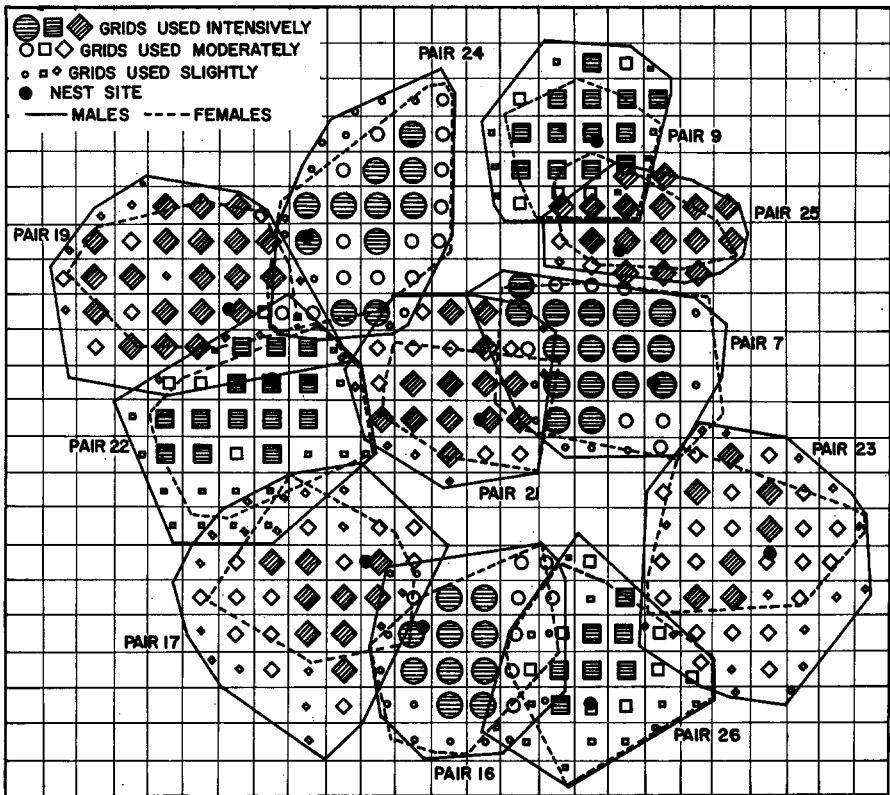
Fig. 2. Location and utilization of total activity spaces of males, location of total activity spaces of females, and location of nest sites of Tree Sparrows on the study area in 1962.

relatively more compressed, and this reduction of the outer cortex tends to increase the area of intense utilization. This pattern of utilization also exists for individuals with differences in total activity spaces in any one year (figs. 1 and 2).

If overlapping of total activity spaces occurred, it generally did so in the area of slight or moderate utilization. This was not invariably true, however (see, for example, males 11 and 16 in fig. 1). There was considerable overlap of activity space between many but not all of the males. Part of this overlap was accounted

TABLE 1

MEAN TOTAL ACTIVITY SPACES, OVERLAP, MEAN DAILY ACTIVITY SPACES, AND POPULATION DENSITY FOR TREE SPARROWS AT EAGLE CREEK, ALASKA

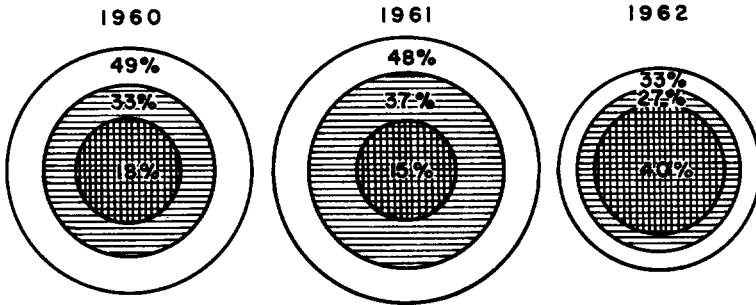|	1960 (9 pairs)	1961 (10 pairs)	1962 (11 pairs)
MALES			
Mean total activity space (acres)	4.5 ± 0.9	5.4 ± 1.5	3.0 ± 0.6
Mean daily activity space (acres)	1.8 ± 0.3	2.7 ± 0.5	1.8 ± 0.4
Overlap of total activity spaces (per cent)	29	10.5	13
FEMALES			
Mean total activity space (acres)	2.2 ± 0.6	2.6 ± 1.3	2.1 ± 1.8
Population density (pairs/100 acres)	28	21	35

Fig. 3. Theoretical models of total activity spaces of male Tree Sparrows showing central area of most intense utilization, and, concentrically outward, areas of moderate and slight utilization. The radii for the theoretic concentric circles were obtained by calculating the radii of circles having an area equal to the mean area of the portions of the total activity spaces used intensively, moderately, and slightly. The area of each concentric ring was then calculated as a percentage of the total area of the outer circle.

for by shifts in area utilized throughout the season and thus much of the area of overlap does not indicate simultaneous use of one area by two male Tree Sparrows. Part of the overlap, however, does represent simultaneous use by two males (fig. 4).

The amount of area used in common between pairs of adjacent birds was measured. This area-in-common was then expressed as a percentage of the sum of the total activity spaces of the pair of Tree Sparrows in question. Where overlap of female activity spaces occurred, it averaged 5 per cent, whereas the overlap of the corresponding adjacent males averaged 7.2 per cent. Where there was no overlap between adjacent females, the overlap between the corresponding males averaged only 2.6 per cent. Thus, overlap between adjacent males tended to be more pronounced when there was some overlap between their females. Since the female activity

TABLE 2

ACTIVITY SPACES OF BANDED MALE TREE SPARROWS THAT RETURNED
TO THE STUDY AREA FOR MORE THAN ONE YEAR[1]

|	Male 4		Male 7			Male 8		Male 9			Male 16	
	1960	1961	1960	1961	1962	1960	1961	1960	1961	1962	1961	1962
Premating	1.0	3.0										
Courting I	2.3	2.8			2.6				4.0			
II		2.1										
Building I		1.6		3.0			3.1		3.7	1.7	1.9	2.0
II				4.1								
Resting									2.0			
Egg laying	2.4		1.9	3.0		0.9			3.3	1.2		
Incubation I	4.1		1.5	2.5	2.6	0.9	1.9	1.6	2.3	1.3	1.6	1.2
II	2.8		1.9	3.0	1.5	1.5	2.7	1.9	3.4		1.9	1.3
III					1.3	2.0			2.5		2.1	1.1
Hatching	1.1											
Nestling I	1.6		2.4	1.6	1.4	1.9	1.4	1.6	3.9		1.8	1.5
II	3.0					2.7		1.9				
Total activity space[2]	5.6	5.4	4.8	5.3	3.1	3.6	4.1	3.6	6.6	2.2	3.7	2.8

[1] When more than one observation period occurred within a stage, the observation periods were numbered I, II, III.
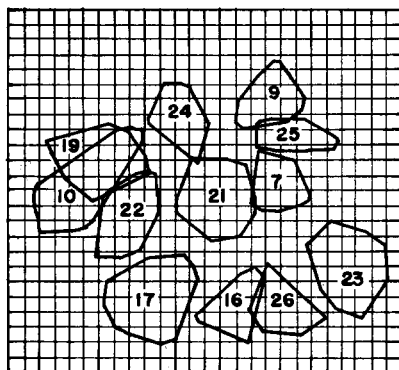[2] Measured from composite maps.
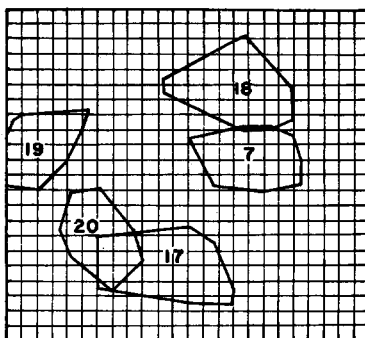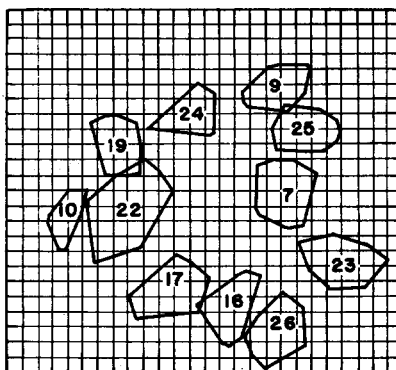
PREMATING STAGE, MAY 17-23
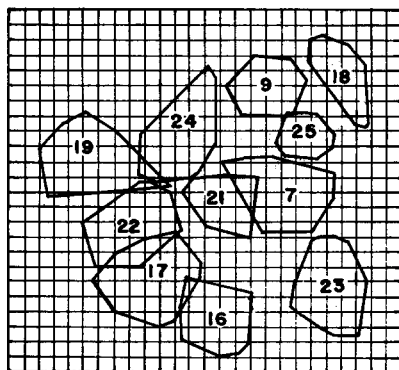
BUILDING-LAYING STAGES, MAY 31- JUNE 4
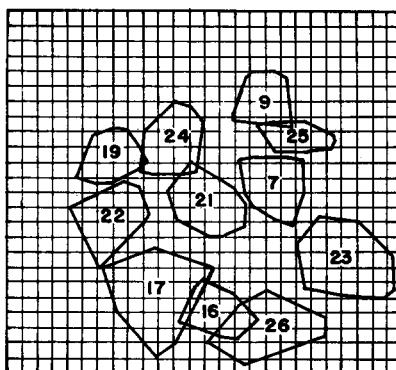
INCUBATION STAGE, JUNE 5-11

INCUBATION STAGE, JUNE 11-17

NESTLING STAGE, JUNE 17-24

Fig. 4. Location of daily activity spaces of male Tree Sparrows on the study area during different stages of the breeding cycle in 1962.

spaces were always situated within those of the males (figs. 1 and 2), it was con-
cluded that the former in large part determines the location of the latter.

The sum of all the overlap of total activity spaces of males was measured and
expressed as a percentage of the total area occupied for each year (table 1). This
value represents a maximum since it includes minor shifts in activity spaces through-

out the season. There apparently is no relation between the size of the total activity space of an individual bird and the amount of overlap on it (figs. 1 and 2). The percentage of overlapping of total activity spaces does not change consistently with population density (table 2).

Examination of figure 4 shows that overlap of activity spaces is greatest early in the season and becomes progressively reduced as the season advances. The reduction in overlap may be caused partly by a progressive reduction in the size of the activity spaces throughout the season and partly by a clearer recognition of boundaries with increased time of residence.

There were significant differences in the mean size of the total activity spaces of the males in each of the three years. These differences were correlated with marked differences in population density of Tree Sparrows (table 1). The approximate population densities of Tree Sparrows for 1960, 1961, and 1962 were 28, 21, and 35 pairs per 100 acres, respectively, while the average total activity spaces were 4.5 ± 0.9, 5.4 ± 1.5, and 3.0 ± 0.6 acres, respectively. Interestingly, the mean of the daily activity spaces was not clearly correlated with population density (table 1). Why this correlation should not carry through to the daily activity is not clear. Possibly there is plenty of area available on any one day so that activity spaces are not confined at the higher densities. Possibly very high densities would place a limit on daily activity space as well.

Females are inconspicuous and spend much of their time on the nest. Thus not as many observation points could be obtained for females as for males. Some of the total activity spaces of the females showed more concentrated activity at the core, much as in the case of the males. This, however, may be due to the fact that an observer is more likely to locate a female near the nest than in any of the other areas the bird might visit.

The total activity spaces of females were smaller than those of their mates and in nearly all cases were entirely within the total activity space of the male (figs. 1 and 2). However, this does not mean that the females are cognizant of the boundaries of male territories. Females do not exhibit territorial behavior. My observations indicate that it is attachment to the nest site and habitual feeding places and the efforts of the males in claiming areas visited by the females that keep the latter confined within the activity spaces of the males.

In those cases where there is overlapping of female activity spaces, it is unlikely that there is any attraction between females. More likely there is an attraction of a female to an adjacent male other than her mate or attraction to the mating activities of an adjacent pair. I have numerous observations of unidentified females appearing in territories of mated pairs. The tendency of the male inhabitant toward such strange females was to court them and frequently mating took place. Often these encounters attracted the attention of the neighboring male that was mated to the philandering female and fights ensued between the males and also between the females. Thus where there is overlapping of activity spaces of males and females, it can be assumed there is some polygamy and polyandry. The extent of overlap and number of visits by both pairs to the area of overlap probably indicates the frequency of occurrence of cross-mating.

The nests were located within the activity spaces of the females (figs. 1 and 2). Frequently, however, they were not centrally located. Nests were never situated within areas of overlap. This might indicate that there is an area around the nest which is inviolate and which is the "center of dominance" for both males and females.
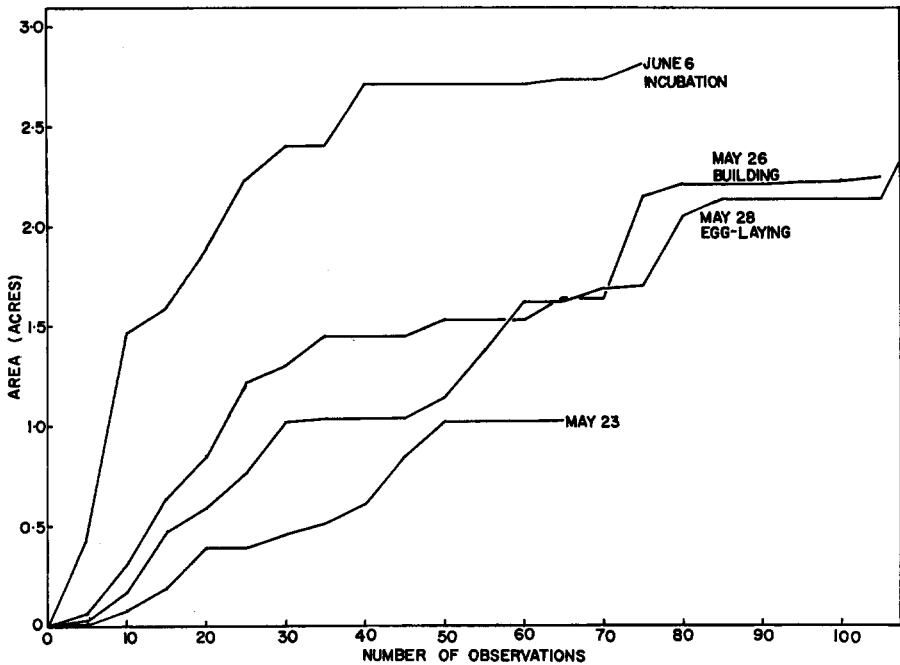
Fig. 5. Some observation-area curves for male 4 at different stages of the breeding cycle in 1960.

The mean total activity spaces of females for the years 1960, 1961, and 1962 were 2.2 ± 0.6, 2.6 ± 1.3, and 2.1 ± 1.8 acres, respectively. The relation between total activity spaces of females and population density shows a similar trend to that of the males, but it is not statistically significant (table 1).

Relation of age to total activity spaces of males.—It has been postulated frequently that age and experience of individuals is a factor in determining the size of territory a male defends, older birds having larger territories than first-year birds in some species. In my study it was possible to color band most of the birds, and there are available several instances of males returning to the study plot for more than one year. Of five males that returned (out of 24 banded), two were present for all three years of the study, and three were present for at least two years. Thus I could compare activity spaces for individual males for successive years.

The data in table 2 indicate that the total activity spaces, from building through nestling, for individual males show the same relative magnitudes as do the mean total activity spaces in the three years of the study (except for male 4). This means that the chief factor influencing total activity space of an individual male is population density or some other extrinsic factor rather than age or experience.

Variations in daily activity spaces throughout the season showed no clearly consistent pattern from year-to-year for the same individual although the data are fragmentary and require further substantiation. If the pattern of variation in daily activity space throughout the season is not consistent from year-to-year for one individual, then we might conclude that the factors controlling the size of territory at any time are not inherent in the individual's genotype directly, or, if so, a
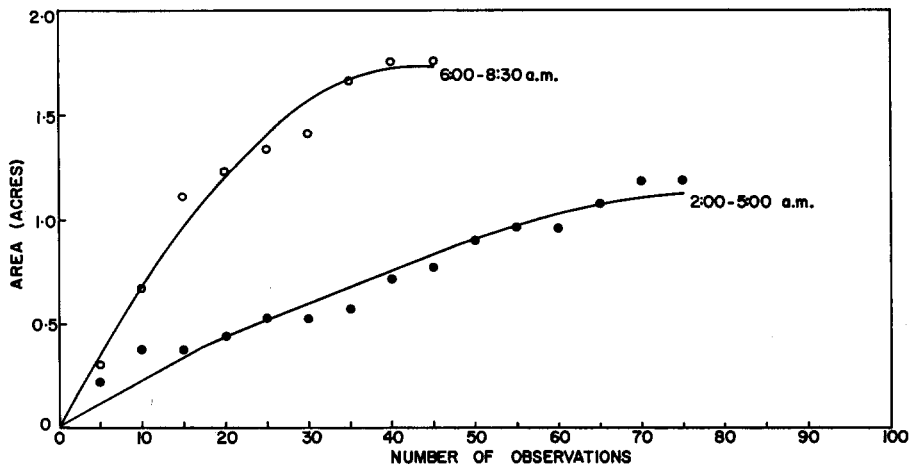
Fig. 6. Two observation-area curves for male 2 plotted at different intervals on the same day, June 9, 1960, when this pair of Tree Sparrows was in the egg-laying stage.

complexity of factors disturbs any regularity of phenotypic expression that might exist.

The diurnal activity cycle.—When cumulative area is plotted after each five observations, the observation-area curve obtained theoretically becomes asymptotic. In practice, however, the asymptotic portion of the curve is reached only infrequently for Tree Sparrows or if it is reached, one can never be sure that the curve will not rise again in a step-like fashion. The latter is a fairly common pattern for the observation-area curve for Tree Sparrows (fig. 5), and it indicates that there were spurts of territorial activity throughout the day with quiescent periods between. This is corroborated with evidence from sample song counts taken every hour throughout the day. Early morning singing was maintained at a high level for from two to six hours, depending upon the stage of the breeding cycle. After this initial singing "plateau" there were quiescent periods alternating with spurts of territorial singing. These spurts of territorial singing became more widely spaced as the day and the season progressed (Weeden, MS).

In 1960 a number of male Tree Sparrows was observed for two periods on a single day, making it possible to plot and compare the slope and level reached by two observation-area curves at different times on the same day.

Some of these paired observation-area curves showed marked differences in form (fig. 6). Some of the pairs reach apparent asymptotes at different levels and thus the points of one per cent change in area (Odum and Kuenzler's arbitrary point of standardization) on the curves would yield different areas for different intervals during the day. Another important difference is the fact that in most cases the slope of the observation-area curve is more gradual during the early morning period than it is later when singing and activity have become less intense. This difference in slope of the curve for different times of day suggests not only a change in the amount of territorial activity but also in its kind. A steep slope indicates longer distances between locations visited than does a gentle slope (Stenger and Falls, 1959). In this case the gentler slope indicates confinement to the core of the

AVERAGE DAILY ACTIVITY SPACES OF MALE TREE SPARROWS FOR EACH
OF THE STAGES OF THE BREEDING CYCLE

	Acres	1960 No. observation periods	Acres	1961 No. observation periods	Acres	1962 No. observation periods
Premating	1.1	2	3.2	5	2.8	2
Courting	2.1	2	3.3	8	3.2	2
Building	1.5	3	2.9	10	2.2	5
Resting	1.3	2	2.8	3		
Egg laying	1.7	5	2.7	4	2.0	5
Incubation	2.1	20[1]	2.5	24[1]	1.8	24[1]
Nestling	2.0	12[2]	2.5	12[2]	1.2	8
Average daily activity space	1.8		2.7		1.8	

[1] All male Tree Sparrows included twice, a few included three times.
[2] All male Tree Sparrows included once, a few included twice.

activity space with more numerous locations short distances apart, whereas a steep slope indicates more lengthy forays into the cortex.

An activity space can be plotted with fewer observations in an interval beginning at 7:00 a.m. than in one beginning at 2:00 a.m. because distances between locations are greater. But in the former the time required to obtain sufficient observations will be longer because the birds are less active (change location less frequently). Also their behavior in the former is more erratic and the curve is more likely to be a series of steps. It was concluded that there was a definite pattern in daily territorial activity beginning on awakening, with visiting, defending, and advertising the core of the daily activity space, followed later in the day by forays into the cortex.

Since these outward forays take place primarily after reaffirmation of the central core, they could be considered as "surplus" activities and the amount of energy available for this "surplus" activity will determine the size of the daily activity space. The amount of energy and time required for reaffirming the core on any one day will depend primarily on the physiologic condition of the birds as well as on the amount of resistance from other males.

In practice it is not possible to measure only the core or only the cortex since they are intricately intermeshed, all times during the day being devoted to some activity in both portions of the daily activity space, differing only in the relative proportion of time spent in each. Thus selecting a standard four-hour interval for observation yields a standardized sample that can be compared for different stages of the breeding cycle.

Daily activity spaces of males throughout the breeding season.—When the mean daily activity spaces for all birds for each stage of the breeding cycle were calculated, a general pattern emerged. The mean daily activity spaces during premating are not quite as large as during courting. The largest premating activity spaces were those established soon after the arrival of the earliest birds, when there was plenty of space available. Thus in 1961 when the observers were present during all of the premating period, the average daily activity space was relatively larger than in the two other years (table 3).

A maximum daily activity space occurred during courting (table 3). This was the time of most intensive activity of Tree Sparrows within the study plot. Most of the males had arrived by this time and were establishing territories and acquiring

mates. The females were wandering through the area, stopping in one male's terri-
tory for a time, then moving on to the next. The male's response to these wandering
females was to follow them as far as possible, presumably to entice them back into
the territory. Adjacent males, of course, were also interested in any females wandering
about and thus came into conflict with other males.

Following courting there was a gradual reduction in the average size of the
daily activity space down through the nestling stage for 1961 and 1962. In 1960
there was a reduction in size of daily activity space until incubation when there
was again quite a considerable increase in average daily activity space. The dif-
ferent pattern in 1960 from the two succeeding years may be because the standard
four-hour observation period during the early morning hours was not adopted in
that year.

Individual birds do not all follow the general pattern indicated by the average
figures in table 3. Some of them may have their maximum activity either later
or earlier than courting and the size of the activity space may fluctuate rather than
decrease gradually. The size of the daily activity space may depend not only on
the physiological condition of the individual male in question but also on the amount
of resistance this individual encounters from the birds adjacent to him.

During building, egg laying, and incubation, the male and female often fed
quietly in close proximity. In order to determine if the activity of the male is
affected by the female, the activity of the female at the nest was studied by a
continuous recording device. The data did not indicate any relation between a
male's attentiveness to the feeding female and his daily activity space during
building, egg laying, and incubation. Neither the total time spent off the nest
nor the number of trips off the nest by the female had any influence on the
size of daily activity space visited by the male. Possibly the time spent by the
male in attending the female during these periods does not appreciably reduce
the energy expended in defending the territory, since he needs to spend some time
in feeding anyway.

DISCUSSION

Clearly the data indicate a direct relation between population density and size
of total activity spaces. Thus, territorial behavior undoubtedly has ecological and
spatial significance.

The relation between the population density and total activity spaces raises the
question, does territorial behavior limit population density, or does population density
limit territory size? The range of population densities in this study apparently were
intermediate because in all three years some seemingly suitable habitat remained
unused. At its upper limit one might expect all suitable habitat to be used, whereas
at its lower limit an increase in the number of free borders might be expected. At
the lower limit of population density we would not expect territory size to increase
indefinitely because of the useless expenditure of energy used in establishing a terri-
tory larger than necessary (Hinde, 1956).

In most species of passerine birds upper and lower limits of population density
are rarely, if ever, achieved, and it is only when these limits are achieved that we
can readily evaluate the significance of the relation between territorial behavior
and population density. Tompa (1962) worked with a very dense Song Sparrow
(*Melospiza melodia*) population and concluded that territorial behavior was the
main factor keeping the population from reaching a disadvantageous level. Kluyver

and Tinbergen (1953) were able to show that territorial behavior limits population densities of Great Tits (*Parus major*) at intermediate levels. Wynne-Edwards (1959) hypothesizes that population densities are limited at a safe level, which will protect the food supply from long-term depletion. Instead of competing directly for food, animals compete for conventional substitutes, for example, territory or social position, which are capable of imposing a ceiling density at the optimum level. This hypothesis fits Kluyver and Tinbergen's (1953) evidence. However, in certain instances (as in the cyclic birds) the optimum population level can be surpassed when conditions are right in spite of territorial behavior. For passerines there must be a number of factors controlling population density and preventing populations from reaching extreme levels. Further, we could postulate that territorial behavior functions differently at different population densities. Such variations in population densities of Tree Sparrows as were encountered in the present study are probably due to annual differences in the time when the habitat becomes available for breeding in the spring and thus are probably very local phenomena. There are a number of ways in which territories of Tree Sparrows could be, and probably are, compressed at higher densities. My data showed that smaller total activity spaces tended to be utilized more intensively, whereas larger ones had a central core of heavy utilization with an outer cortex that was used less intensively. Possibly the outer cortex of less intense utilization could be abandoned altogether under high population density.

A study by Conder (1956) of territory in the Wheatear (*Oenanthe oenanthe*) showed a similar relation between territory size and population density as was found for the Tree Sparrows. In his study a limit of compressibility of territory size for the Wheatear was reached. In the year of highest density, the birds occupied some relatively unsuitable habitats that were not utilized at lower densities.

In my study of Tree Sparrows there was no expansion into unsuitable habitats at the population densities encountered. Apparently, compression of territories is the manner in which denser populations are accommodated.

It is interesting to note that daily activity space was not proportional to population density (at the population densities studied). It was the same (1.8 acres) for 1960 and 1962 when densities were 28 and 35 pairs per 100 acres, respectively, but it was considerably higher (2.7 acres) for 1961 when population density was lowest (21 pairs/100 acres). Possibly the daily activity space cannot be compressed below a certain limit, and it is not inconceivable that this minimum daily activity space approaches in value the minimum total activity space that can be tolerated.

Another way in which Tree Sparrows could accommodate to high population densities is to allow territories to overlap. We had evidence of considerable overlap for some of the birds (1960). Since both overlap and reduction of the outer cortex of the total activity space have been observed for the Tree Sparrows, it is likely that these are the ways in which high density will affect the Tree Sparrow population rather than that territorial behavior will place a limit on population density.

At the price of treading dangerous ground, we might look to the cyclic birds for an understanding of how territorial behavior functions at very high and very low population densities. Among Rock Ptarmigan (*Lagopus mutus*) at very low densities (one pair/square mile) males have no contacts with other individuals of the same sex and thus are not called upon to defend a territory. Thus it is not possible to determine whether they live within the context of a territory or not (R. B. Weeden, personal communication). Parmelee and MacDonald (1960:29) noted that male Rock Ptarmigan on Ellesmere Island at low population densities

"seemed to be on territory, but these areas were not openly defended with so few birds about." These authors also noted very few courtship flights at densities of one pair per square mile. Possibly, then, territorial behavior ceases to operate at very low densities in the Rock Ptarmigan. It seems that breeding can be successful without the social stimulation imposed by territorial activity. Among passerines there are examples of successful breeding in situations where only one pair of birds inhabits small islands (Beer, Frenzel, and Hansen, 1956). Red-backed Shrikes (*Lanius collurio*) occasionally are not compelled to defend the area in which they live and breed when there are no other shrikes in the vicinity. In such a situation the boundaries are less rigid than when there is defense against other shrikes (Durango, 1956). Breeding may conceivably be more successful without territorial activity since populations may be on the increase at very low densities for cyclic animals such as the ptarmigan.

At very high population densities (150–200 pairs/square mile) of Willow Ptarmigan (*Lagopus lagopus*) territorial behavior still operates even though it results in confusion rather than in regulation of population structure. Under such high densities males are constantly called upon to defend their territories and they respond to this constant stimulation by reacting to transgressions less often (R. B. Weeden, personal communication). The females also show a change in behavior at these high densities, having a greater flushing distance from the nest than at intermediate densities.

Thus territorial behavior may have a two-fold function. At very high densities it may place a limit on breeding success of some species, while at intermediate densities it may serve to partition out the available habitat and the available resources. The pair bond and the partitioning out of the habitat may provide a framework in which the breeding activity can be adjusted to the phenology with the least expenditure of energy.

In both the Tree Sparrow and the Ovenbird there was a great deal of individual variation in total activity space as well as in daily activity space. For Ovenbirds this individual variation was related to food availability (Stenger, 1958) but in that species boundaries of territories were more clearly defined with definite buffer zones between territories. For Tree Sparrows there were no buffer zones between territories, the rather diffuse boundaries abutting directly or even overlapping. Thus the territory of a male Tree Sparrow is more directly dependent on the territorial activity of the males around him. Each male Tree Sparrow forms a unique situation with each of his neighbors, resulting in either a small or a large amount of elasticity in the "border" between them. A line is undoubtedly established at the points of balance (Hinde, 1956). An individual male may have up to five neighbors (usually three to four) and his daily activity space is the resultant of up to five unique situations changing daily. Thus, territorial behavior must be considered in the context of an extremely complex social and physiological system.

SUMMARY

Spatial relations in territorial behavior were intensively studied for 30 pairs of Tree Sparrows (*Spizella arborea*) in central Alaska. The two chief aspects of spatial relations studied for each pair were total activity spaces throughout the season (combining all observation points) and daily activity spaces (locations visited by the pair in a four-hour observation period on a single day).

Total activity spaces for males ranged from 1.5 to 9.3 acres. The mean size of

the total activity space differed in each of the three years of the study and reflected differences in population density. For 1960, 1961, and 1962 mean total activity spaces were 4.6, 6.0, and 3.4 acres, respectively, for population densities of 28, 21, and 35 pairs per 100 acres, respectively. Total activity spaces generally had a central core of more concentrated use and an outer cortex where visits were less frequent. This pattern was more pronounced for larger activity spaces than for smaller ones. Some overlapping of total activity spaces occurred in the cortex portion. Some of this overlap was due to shifting of activity spaces throughout the season while some of it was due to simultaneous use of an area. The amount of overlapping in any one year bore no relation to population density.

Size of total activity space of males was not influenced by age of individuals.

Total activity spaces of females were not related to population density. Their total activity spaces were smaller (range 0.6–4.4 acres, mean for the three years 2.2, 2.6, and 2.1 acres, respectively) than for males and were situated entirely within the total activity spaces of the males.

Territorial behavior differed in kind and intensity throughout the day. The diurnal cycle began by reaffirmation of the core through advertisement (song) followed later in the day by more lengthy trips into the cortex.

In general, daily activity space was maximum during courting and decreased gradually throughout the season. There was some variation in the general pattern for individual birds, some reaching their maxima either before or after courting, some even fluctuating throughout the season.

Average daily activity space showed no direct correlation with population density.

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