THE UTILIZED TERRITORY OF THE OVENBIRD

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HANN (1937) showed that the Ovenbird (*Seiurus aurocapillus*) strongly exhibits territorial behavior. Since the area defended by the male is used for mating, nesting, and as a feeding ground for adults and young, it exemplifies type A of Nice's (1941) classification.

We studied territories of Ovenbirds in four forest types at the Wildlife Research Station of the Ontario Department of Lands and Forests, in Algonquin Park, Ontario. Observations were carried out during the summers of 1955 and 1956. This paper deals with the extent of the area utilized by a male Ovenbird during the breeding season, some aspects of the way in which it is utilized, and the variations in size which occur in this area as the breeding season progresses.

DESCRIPTION OF STUDY AREAS

Five plots for the study of territories of Ovenbirds were established in four forest types as follows: one plot in aspen, one in a conifer–birch association, two in a mixed hardwood–conifer association, and one in mature maple forest. One of the mixed plots was used only in 1955, and was so similar to the other that it will not be described in detail. The conifer–birch plot was used only in 1956. Each plot was surveyed into a grid of 66-foot squares and the intersections were marked. Areas of plots used varied from eight to 20 acres.

Differences in tree species and differences in number, height, and density of canopy layers were used to map study plots into cover types by inspection. Within each cover type circular areas of 33-foot radius were chosen arbitrarily. These samples, which included from eight to 16 per cent of the area in each plot, were used to estimate height, density (percentage of sky obstructed by foliage, not allowing for spaces between leaves), and species composition of each stratum of the forest. In addition, species and diameter at breast height (DBH) of all trees more than 1.5 inches in diameter were recorded.

Millacre quadrats (6.6 feet square) located at the grid intersections were used to estimate percentage of ground covered by logs and rocks, and by each species in the low vegetation.

Brief descriptions of the four main study plots are given below. The percentage of trees in the canopy made up by each of the commoner species is included.

Aspen Plot.—Upper canopy 93 per cent aspen (*Populus tremuloides, P. grandidentata*). Lower canopy 37 per cent maple (mainly *Acer rubrum*), 28 per cent white spruce (*Picea glauca*), and 23 per cent balsam fir (*Abies balsamea*). Brush layer denser than in other plots and composed mainly of hazel (*Corylus cornuta*) and small conifers. Common ground plants—bunchberry (*Cornus canadensis*), bracken (*Pteridium aquilinum*), and sarsaparilla (*Aralia nudicaulis*). Leaf litter mainly of broad leaves.

Conifer–birch Plot.—Upper canopy 39 per cent white birch (*Betula papyrifera*), 20 per cent aspen, and 32 per cent white pine (*Pinus strobus*). Lower canopy 71 per cent balsam fir. Brush of hazel and small conifers. Common ground plants—bracken, bunchberry, sarsaparilla, blueberry (*Vaccinium angustifolium, V. myrtilloides*), and grasses. Leaf litter mainly of pine needles.

Mixed Plot.—Variable. Parts resemble all other plots. Large areas of mature hardwood and other areas of pure conifer. Upper canopy 37 per cent white birch, 23 per cent red and sugar maples (*Acer rubrum, A. saccharum*), and 13 per cent white spruce. A few large specimens of yellow birch (*Betula lutea*), white pine, and hemlock (*Tsuga canadensis*). Lower canopy, present in only 34 of 42 samples, mainly of balsam fir (36 per cent), maples (20 per cent), white spruce (19 per cent), and white birch (12 per cent). Brush layer, present in only half the samples, chiefly of hazel, striped maple (*Acer pennsylvanicum*), and small conifers. Common ground plants—bunchberry, bracken, sarsaparilla, maple seedlings, dewberry (*Rubus pubescens*), and grasses.

Maple Plot.—Most complex canopy of any plot, having three layers all dominated by sugar maple, 85 per cent in upper and lower canopy, and 91 per cent of understory. Beech (*Fagus grandifolia*), 12 per cent of upper canopy. Some ironwood (*Ostrya virginiana*) in all three canopy layers. Lower canopy and understory present in 10 and 12 out of 17 samples, respectively. Brush present in only three of 17 samples, chiefly of striped and sugar maples. Ground vegetation mainly of tree seedlings—sugar maple, striped maple, and beech. More logs and deeper leaf litter than in other plots.

Table 1 shows the height and density of each stratum of the forest in each of these plots. Table 2 shows the composition of the forest. Trees are classified with regard to tolerance (here taken to mean capacity to develop and grow in the shade of and in competition with other trees) following Toumey and Korstian (1947).

When study plots are arranged in the order—Aspen, Conifer–birch, Mixed,

TABLE 1

HEIGHT AND DENSITY OF EACH STRATUM OF FOREST IN STUDY PLOTS

Strata	Plots			
	Aspen	Conifer–birch	Mixed	Maple
Height (feet)[1]				
Upper canopy	45	50	55	85
Lower canopy	25	25	25	35
Understory	—	—	—	17
Brush	8	5	6	4
Ground vegetation	1.5	1.5	1.5	1
Density (per cent covered)[1]				
Upper canopy	50	45	65	75
Lower canopy	20	15	20	85
Understory	—	—	—	40
Brush	50	30	25	25
Ground vegetation	70	70	45	5
Logs and rocks	5	5	10	10

[1] Median values are used for height and density.

TABLE 2

COMPOSITION OF FOREST IN STUDY PLOTS

Species[1]	Trees[2] per acre				Saplings[3] per acre			
	Aspen	Conifer–birch	Mixed	Maple	Aspen	Conifer–birch	Mixed	Maple
Tolerant								
Sugar and red maple	70	0	46	182	71	0	10	83
Striped maple	0	0	2	5	0	0	7	6
Ironwood	3	0	3	13	0	0	1	17
Beech	0	0	0	19	0	0	0	1
Balsam fir	53	141	58	0	39	79	21	0
Spruce (mainly white)	69	28	43	0	37	8	6	0
Hemlock	0	0	9	5	0	0	0	0
Intermediate								
Yellow birch	0	0	10	0	0	0	0	0
Pine (mainly white)	1	66	20	0	0	2	1	0
Intolerant								
Aspen (mainly trembling)	378	40	2	0	25	0	0	0
White birch	10	80	64	0	9	2	2	0
Willow sp.	0	0	0	0	7	0	0	0
Totals	584	355	257	224	188	91	48	107
Per cent composition								
Tolerant	33	47	62	100	78	96	94	100
Intermediate	0	19	12	0	0	2	2	0
Intolerant	67	34	26	0	22	2	4	0

[1] Three species that had fewer than five stems per acre in any plot are omitted.
[2] Trees have DBH over 2½ inches.
[3] Saplings have DBH 1½ to 2½ inches.

Maple, a number of trends are apparent. Height and density of the upper canopy increase while density of brush and ground cover decreases from Aspen to Maple (Table 1). Number of trees per acre and the proportion of trees made up by intolerant species decrease (Table 2). On the other hand, the proportion of trees belonging to tolerant species increases. A high proportion of saplings is tolerant in all plots.

These trends suggest that the plots represent an early stage (Aspen), two intermediate stages (Conifer–birch, Mixed), and a late stage (Maple) in forest development. However, they probably do not represent stages in a single succession. The Aspen and Conifer–birch Plots seem likely to become more coniferous. These stands may be regarded as local representatives of the boreal forest. The Mixed and Maple Plots will likely continue to support mixed or hardwood stands. This is not surprising since Algonquin Park lies in a transition zone between the boreal forest and the northern conifer–hard-

wood forest (as described by Brown and Curtis, 1952), and stands of both types are found on different sites within the area (Halliday, 1937).

Method Used to Study Territory

Territorial disputes between male Ovenbirds were observed from the time the birds arrived on the breeding grounds until after the young had left the nest. Most encounters consisted of chasing and vocalizing (call notes and songs) or only vocalizing, although physical contact was occasionally observed. Disputes were fewer, shorter, and less vigorous as the breeding season advanced. Not enough territorial disputes were observed to outline the area defended by any individual, i.e., to measure territory in the strict sense.

Instead, all locations where a male was observed were plotted and used to estimate the area utilized by that bird. Many of these locations were estimated when a bird was heard singing.

Occurrence of song distinguished males from females which are similar in plumage but do not sing. A few birds were marked with colored bands, but individual males were identified chiefly by differences in their songs. Tape recordings were useful for verifying identifications. Detailed analyses of songs will be published elsewhere.

Nine males were studied in 1955, and 13 in 1956. One observer watched a bird, taking care not to disturb it. When the bird was located, its position was marked on a map, and the height at which it was observed was recorded. Locations on the map were numbered consecutively. Each bird was studied one day a week, which amounted to eight or nine times during the breeding season in 1956. Fewer observation periods were completed in 1955. The observation period each day extended from 4:15 to 5:45 a.m. E.S.T. in 1955, and from 5:15 to 9:30 a.m. E.S.T. in 1956.

Total Territory Utilized During the Breeding Season

All locations where each male Ovenbird was observed from the arrival of its mate until its young left the nest were mapped as in Fig. 1. For each bird most of the points formed a compact group, but a few points (about five per cent) lay well outside this group. In order to determine the *total utilized territory*, the five per cent of points that were most isolated were rejected in all cases. Peripheral points of the remaining group were joined to form a polygon having no indentations (Fig. 1). Three of the birds (M 26, M 27, M 30) were not observed in certain open areas that lay within the polygons, and these areas were subtracted in finding the area of the total utilized territory. Areas were obtained from the maps using a compensating planimeter.

Points obtained during the premating period were excluded because there was sometimes a shift in the location of a territory when the female arrived. Points obtained after the young left the nest were excluded for two reasons. In the first place, the family group breaks up (Hann, 1937), and it is doubtful

whether most males still exhibit territorial behavior. Secondly, young birds were apparently not cognizant of the boundaries of the adult's territory and sometimes wandered beyond, in which case the male went beyond the boundary to feed them.

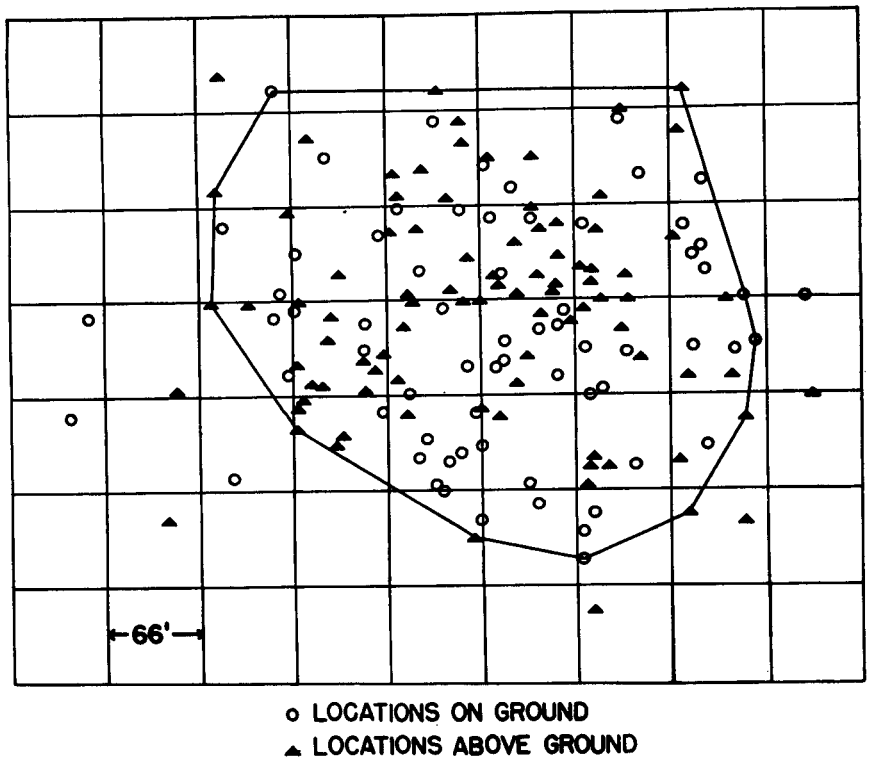

FIG. 1. Total utilized territory of M 20. Locations where the bird was observed are shown.

The *total utilized territory* as determined above is not necessarily identical with the area that a bird will defend if called upon to do so. However, it is an estimate of the area used during the breeding season by a male exhibiting territorial behavior. It is the segment of the environment in which most of the activities associated with the reproductive cycle are performed.

Distribution of activities.—Locations where male Ovenbirds were seen or heard did not appear to be concentrated anywhere but were scattered throughout the total utilized territory. Data for M 20 shown in Fig. 1 are typical in this regard. Most points represented locations where a bird sang in the trees but no particular song posts were used repeatedly. Prolonged vocalization occurred in any part of the territory where there were trees (usually deciduous)

of a suitable height (Fig. 1). The Ovenbird feeds almost entirely on the ground (Stenger, 1958), and nearly all observations of a bird on the ground represented feeding activity. When these observations are plotted separately (Fig. 1) they too are seen to be scattered throughout the territory.

Unforested areas that appeared to be similar to each other were used by some birds but not by others. Large open areas of bracken and grasses in the Aspen Plot were not used by M 26 and M 27, whereas M 23 and M 24 in the Conifer–birch Plot were observed to use similar areas. M 30 in the Maple Plot did not utilize an open wet area.

The total area utilized by a female was not determined. However, a female was sometimes observed in company with a male or was flushed from its nest and could then be followed. Females were not observed beyond the boundaries of their mates' territories. However, they did not appear to take an active part in defense of the territory. The nest was located within the total utilized territory although often near the edge.

Buffer zone.—When total utilized territories of neighboring birds are drawn on a map there is usually a *buffer zone* (Williamson, 1956) between them. An example is shown in Fig. 2 where all the territories except those of M 4 and M 5 were separated by approximately 60 feet. In the Maple Plot, where territories were largest, the buffer zone was about 100 feet wide.

Sometimes there appears to be considerable overlap between adjacent territories as illustrated in the Mixed Plot in 1956 (Fig. 3). This results from shifting of territories during the breeding season; territories utilized by adjacent birds on any one day were always well separated.

Most of the points rejected in the estimation of total utilized territory occurred in the buffer zone. When a bird was observed in the buffer zone it either did not sing at all or gave one or two weak songs. These observations suggest that Ovenbirds recognize the boundaries of their territories since they behave differently in the buffer zone than inside the total utilized territory.

Extent of the total utilized territory.—All the birds that were studied occupied fairly compact territories approximately circular or oval in shape (Figs. 1–3). The size of these areas varied considerably as shown in Table 3. The total utilized territories of M 5 and M 7 were smaller when they were unmated than when they were mated. When birds renested (this occurs only when the first attempt at nesting fails) they occupied larger territories in two cases (M 5, M 32) and a smaller territory in one case (M 28) than during the first attempt at nesting. They did not change location, however (Fig. 3).

The greatest differences in size of territory occurred among different forest types. Considering first nesting attempts in 1956, for the 11 birds for which comparable data are available (omitting M 7 and M 32), the average sizes of territories in the different plots are: Aspen 1.8 acres; Conifer–birch 2.2 acres; Mixed 2.4 acres; and Maple 3.3 acres. The same trend is shown in 1955

for the Aspen, Mixed, and Maple plots. It was pointed out in the section dealing with study areas that when the plots are placed in this order they show a number of trends in the structure and composition of the forest. Thus, territory size increases as canopy height and density increase, as brush and ground vegetation decrease, and as the forest changes from an early seral stage with many intolerant trees, to a late stage in development characterized by fewer but more tolerant trees. These trends are quite marked when the territories in different plots are compared, but do not hold in every case within plots. These features of the habitat may affect the behavior of the birds, or may determine differences in the supply of food available to Ovenbirds, or both. The relationship between available food and size of territory is considered in a separate paper (Stenger, 1958).

Height of the territory.—The space occupied by a bird is a volume rather than an area and has a measurable height. It can be argued that a more accurate account of territory might be attained by comparing volumes. This

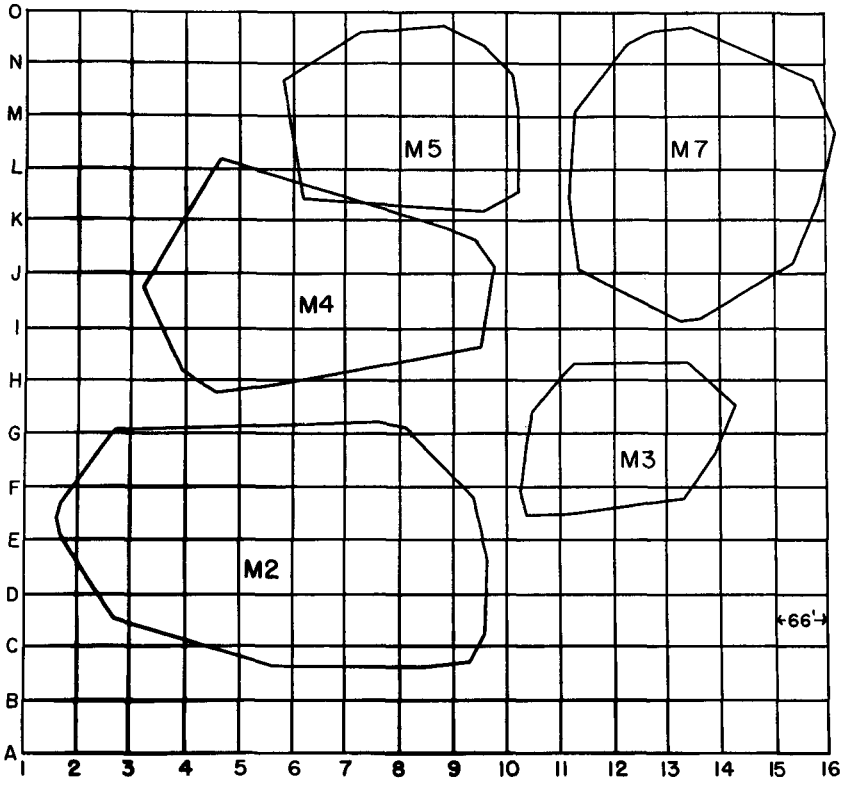

FIG. 2. Total utilized territories in Mixed Plot in 1955.

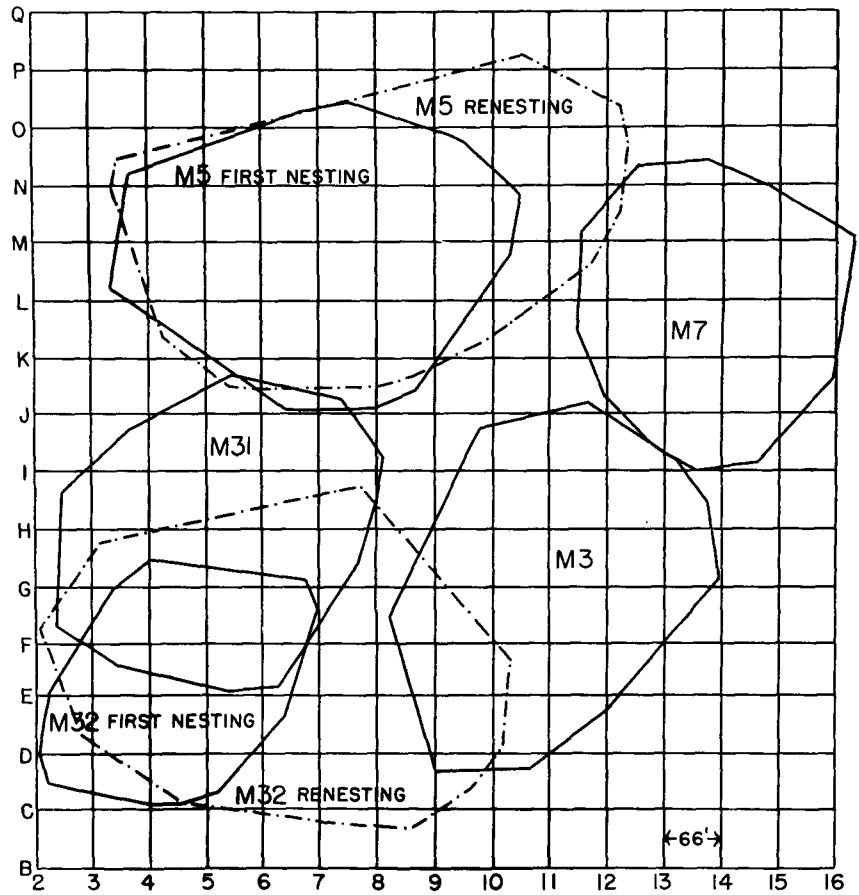

FIG. 3. Total utilized territories in Mixed Plot in 1956.

would necessitate measuring the height of each territory. Greater height might compensate for smaller area or height might be related to area in some other way.

The height of the space occupied by a male Ovenbird was estimated by finding the average height of the highest 25 per cent of points where the bird was observed. Analysis of data from territories of nine Ovenbirds showed that the vertical extent of activity was a little less than the height of the densest layer of the forest canopy. This resulted from the fact that Ovenbirds usually sang from the lower branches of the canopy. The vertical extent of activity was not clearly related to the area of the territory. Height values were less variable than areas of territories and did not compensate for them. Thus, if

volumes were calculated from these dimensions, they would be more variable than the corresponding areas.

These results, together with the fact that this species feeds and nests on the ground, indicate that, for the Ovenbird, the area of the total utilized territory is more meaningful than the volume of space occupied.

TABLE 3

VARIATION IN SIZE OF TOTAL UTILIZED TERRITORY AMONG FOREST TYPES

Forest type	1955		1956		
	Bird	Territory (acres)	Bird	Territory (acres)	
				First nest	Renest
Aspen	M 15	1.0	M 28	1.5	1.1
			M 26	1.9	
			M 27	2.1	
Conifer-birch			M 24	2.1	
			M 20	2.2	
			M 23	2.2	
Mixed	M 5[1]	0.8	M 5	2.7	3.6
	M 9	1.6	M 31	2.2	
	M 4	1.7	M 3	2.4	
	M 7	2.0	M 7[1]	1.8	
	M 10	2.1	M 32	1.5[2]	3.4
	M 2	2.8			
Maple	M 12	3.9	M 30	2.5	
	M 13	4.3	M 29	4.0	

[1] Unmated.
[2] Based on observations on only two days.

CHANGES IN UTILIZED TERRITORY AS THE BREEDING SEASON ADVANCES

A distinction can be made between the total utilized territory for the breeding season and the area utilized on one day. Changes in the area utilized daily may be observed as the breeding season advances.

The observation-area curve as a means of estimating utilized area.—Odum and Kuenzler (1955) used the observation-area curve as a standard method of measuring size of territory for comparative purposes. After each 10 consecutive observations were mapped, they plotted the area outlined by all the observation points against the total number of observations. At first, the area increased as more observations were included, but later the curve leveled off. Odum and Kuenzler selected as a standard, for comparison of different territories, the area obtained when there was less than one per cent increase in area for each additional observation.

This method has been modified and extended for the treatment of Ovenbird

data. Instead of mapping the location of a bird every five minutes, as Odum and Kuenzler did, all different locations where a bird was observed were recorded. This resulted in approximately 12 to 15 locations per hour. Points were plotted on the observation-area curve after each five consecutive observations.

In the present study there were a number of days when the birds were inactive. On such days, the number of locations visited by a bird were too few to reach the level portion (or the level of one per cent change) of the observation-area curve. Since the area utilized can change substantially from one day to the next in the case of the Ovenbird, there seemed to be no justification for combining observations made on different days and in different weeks. In order to reach the one per cent level on the observation-area curve, 60 or more locations were usually required and this number was obtained only two or three times for each bird during the breeding season. It was relatively easy, however, to obtain 30 to 40 locations on any one day. As few as 20 locations were sufficient to estimate the slope of the initial portion of the observation-area curve. This slope was estimated by calculating a line of best fit to the points on the initial portion of the curve.

The slope of the initial part of the observation-area curve is proportional to the area reached at the level portion of the curve. This is shown in Fig. 4, in which slopes of the initial portions of the curves are plotted against the final areas for all those occasions when the level portion of the curve was attained (at least the last three points at the same level). Points on the level portion of a curve were excluded in calculating the slope.

The relationship shown in Fig. 4 means that the rate of increase in area per observation is greater when the area is larger, and suggests that successive locations at which an Ovenbird is observed may be farther apart when the bird visits a larger area. This was tested by measuring the distances between consecutive observation points and comparing the mean distance obtained with the area reached at the level portion of the observation-area curve. Fig. 5 shows that distances between points were greater when the area utilized was larger.

Thus, there is a reasonable basis for relating the slope of the initial portion of the observation-area curve to the final area reached by the curve. This relationship was used to estimate the areas utilized by Ovenbirds on days when only enough data were obtained to calculate the slope of the initial portion of the curve. A line of best fit was calculated for the data in Fig. 4. Given a slope value, a corresponding area can be read from this graph or calculated from the equation of the line, $Y = .005 + .0199X$.

Estimates of utilized area obtained in this way should not be regarded as very accurate in view of the rather wide scatter in Fig. 4. Since the error is likely to be greater if the area is large, no definite values were assigned to

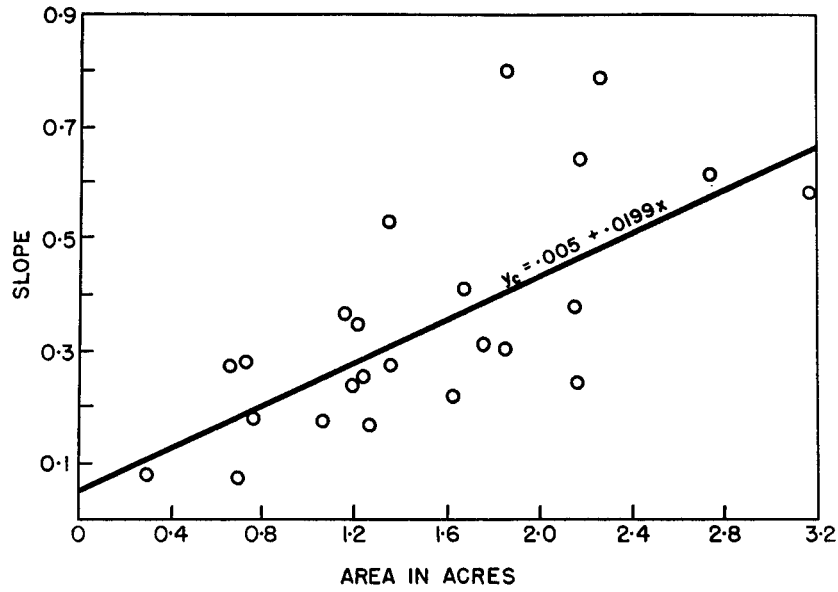

FIG. 4. Relation between slope of the initial portion of the observation-area curve and the final area reached by the curve. The line of best fit to these data is shown.

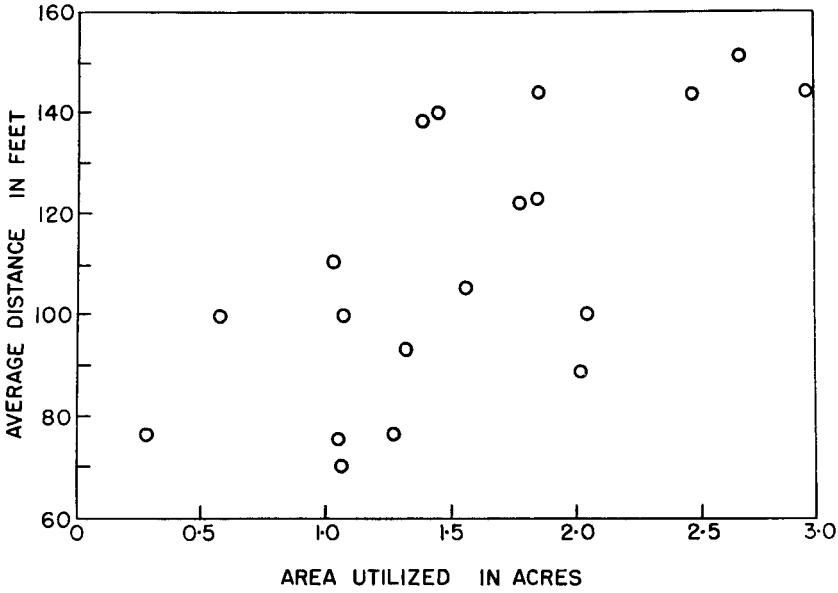

FIG. 5. Average distance between successive locations at which a bird was observed in relation to area utilized. Area utilized is taken to be the area reached at the level portion of the observation-area curve.

estimated areas in excess of four acres. This method made it possible to use data which would otherwise have been rejected as incomplete.

Changes in the area utilized by the male during the reproductive cycle.—The duration of the different stages of the breeding cycle were determined for a few Ovenbirds whose nests were found. Where nests were not found young birds were easily discovered after they had left the nest and could be aged approximately. Data on the breeding cycle obtained in this way agreed with the more extensive information given by Hann (1937); therefore his time intervals were used to fix approximate dates of the different stages of the breeding cycle for birds where only the young were found.

The following is a brief summary of the Ovenbird's breeding cycle:

Premating	—period from arrival of male to arrival of female; about 13 days in 1955, and about 18 days in 1956.
Mating	—a period of variable length from arrival of female until nest-building begins.
Nest-building	—5 days for first nest, 4 days for renesting.
Egg-laying	—3 to 5 days, depending on number laid.
Incubation	—12 days, beginning with second-last egg.
Nestling	—7 to 9 days.
Young leave nest	—young leave nest in about 9 days, fly in about 11 days, and are independent about 30 days after hatching.

Using the method outlined in the previous section, the area utilized by each bird in each observation period was estimated and the values obtained were assigned to the appropriate stages of the breeding cycle. These values, expressed as fractions of the total utilized territory, are shown in Fig. 6 for the 11 birds for which the necessary data were available. Since no one bird was studied during every stage of the breeding cycle, all the values obtained in each period were averaged and are shown in the final histogram. In interpreting these histograms, it must be borne in mind that measurements were not made at precisely the same stages for all the birds, even within the main periods of the breeding cycle.

Two major peaks in the size of the area utilized occurred during the breeding cycle (Fig. 6), one during the premating and mating periods, and the other during the incubation and nestling periods. During these two peak periods the average area utilized by the male in one day was almost as large as the total utilized territory. During the period between these peaks (nest-building and egg-laying) the average area was about half the size of the total utilized territory. These marked variations in area utilized can be explained in terms of the male's activities.

In the premating period, when the area utilized is large, the male establishes his territory. He sings often and encounters with other males are frequent. Six of eight males for which data are available showed an increase in area

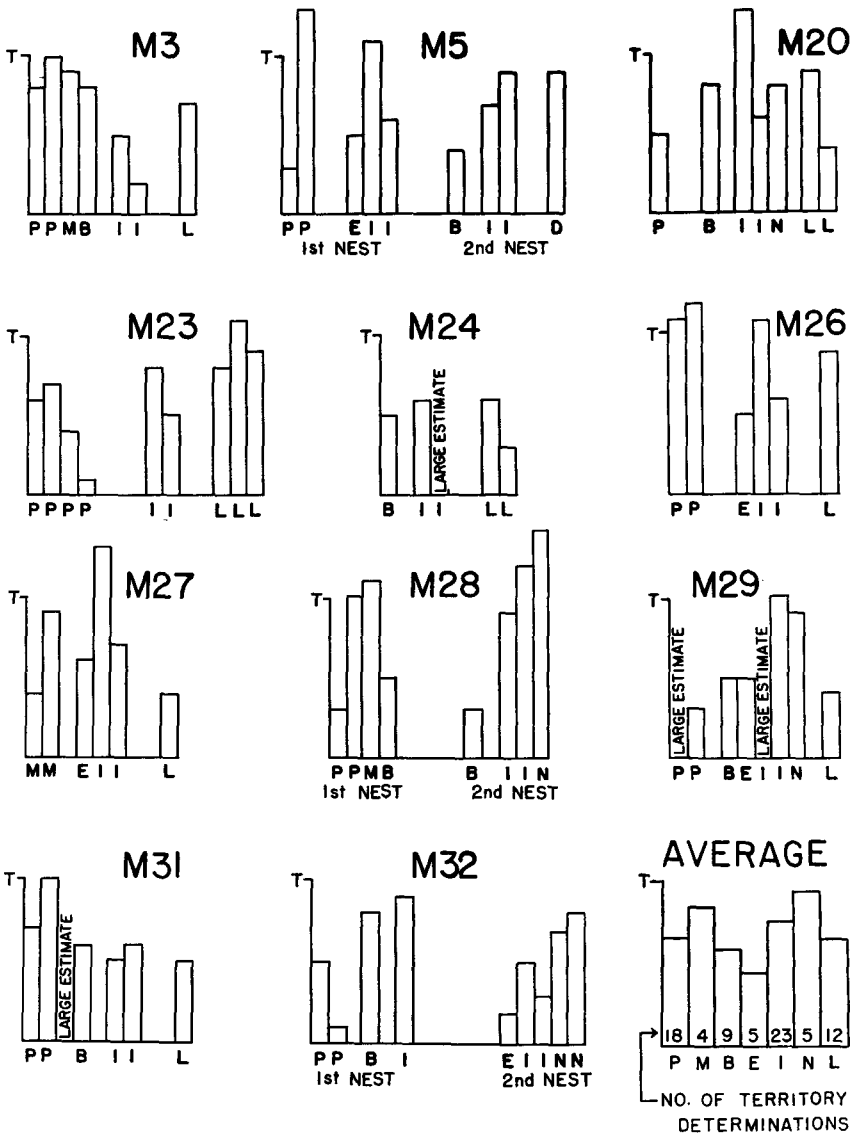

FIG. 6. Area utilized in different periods of the reproductive cycle expressed as a fraction of the total utilized territory (T) for each bird. Average values for all birds for each period of the reproductive cycle are given in the final histogram. Periods of reproductive cycle: premating (P), mating (M), nest-building (B), egg-laying (E), incubation (I), nestling (N), and after young have left nest (L).

utilized during this period. One bird (M 23) that had an extended premating period showed a decrease in the area utilized following the initial increase.

Three males were studied in the period between the arrival of the females and the beginning of nest-building. In this mating period the area utilized by the male was large.

From the time the female began building the nest until she started to incubate, the area utilized by the male was small (less than in earlier periods in 6 out of 8 cases). In this period the male sings infrequently and is often seen with the female although he does not help build the nest. Copulation takes place mainly in this period (Hann, 1937).

During the incubation period, the area utilized once again increased in 10 out of 12 cases. The male does not take part in incubation and is seldom seen with the female at this time. He sings about as often as during the premating period. Most males (8 out of 12) showed a small decrease in area utilized toward the end of this period.

During the nestling period the male helps feed the young. He sings infrequently and is secretive, and is therefore difficult to observe. Adequate data were obtained for only four birds, all of which utilized areas about as large as, or larger than during the incubation period.

When the young leave the nest the brood is divided between male and female. In this period some males (5 out of 10) utilized larger areas than previously, whereas others used smaller areas. If there are several young they tend to disperse rather than to stay together. It may be that males tending more than one young utilized a larger area during this period than those tending a single young bird.

Thus, the size of the area a male Ovenbird utilizes varies during the breeding season. It is large when he is occupied with territorial defense, advertising song, and food gathering for the young, and small when he spends his time with the female and copulation is frequent. While the areas utilized by males change markedly, no conclusions concerning the area utilized by females, or changes in size of defended territories can be drawn from the data presented in this paper.

Apparently the Ovenbird is somewhat different from certain other species in regard to changes in size of the territory occupied as the breeding season progresses. Young (1951) thought that territories of the Robin (*Turdus migratorius*) shrank progressively as the breeding season advanced, while Odum and Kuenzler (1955) found that for a number of species territories were smaller during the nestling stage than during nest-building and incubation.

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SUMMARY

Territories of Ovenbirds were studied in four forest types in Algonquin Park, Ontario. Locations where a male was observed were used to estimate its *total utilized territory* for the breeding season. Birds were observed singing or feeding in all parts of their territories, although some birds did not utilize open areas. Total utilized territories of adjacent males were usually separated by a buffer zone but occasionally overlapped. However, areas used by adjacent males on any one day were always separated.

Total utilized territories varied from 0.8 to 4.3 acres, being small in an aspen stand, intermediate in size in conifer–birch and mixed stands, and large in a maple stand. Thus, the size of the territory increased with increasing height and density of forest canopy, and with decreasing vegetation near the ground. Unmated birds had small territories.

The vertical extent of each bird's activity was related to the height of the forest canopy where the bird sang, but not in any regular way to the area of its territory.

A method was developed to compare the areas utilized by male Ovenbirds on different days during the breeding season. The area utilized was large during the premating and mating periods, smaller during nest-building and egg-laying, and large again during the incubation and nestling periods. Thus, the area utilized by a male Ovenbird is large when he is occupied with territorial defense, song, and feeding the young, and small when he is often with the female and copulation is frequent.

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