

MINIMUM SPACE REQUIREMENTS OF SOME NESTING PASSERINE BIRDS

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MANY workers concerned with the problems involving home range and territorial behavior in vertebrates consider space to be one of the more important facets. It is believed that a minimum amount of space is required by an individual or pair before it will occupy an area even though the area may contain apparently adequate nesting cover, escape cover, food, song perches and other specific requirements for survival and perpetuation of the species.

The Quetico-Superior Wilderness Research Center provided facilities for us to conduct investigations on the ecology of the vertebrates found in the vicinity of Basswood Lake, Lake County, Minnesota. This is paper No. 3419 of the Scientific Journal Series from the Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. We here report on the data gathered on the space requirements, during the nesting season, of the Song Sparrow (*Melospiza melodia*), Yellow Warbler (*Dendroica petchia*) and the Red-eyed Vireo (*Vireo olivaceus*) during the six field seasons, 1950 to 1955, inclusive.

The Basswood Lake area, with its many islands (Fig. 1), is well suited to the study of the minimum area that birds require. Many of the islands are situated so that the birds resident thereon do not have ready access to the mainland or to other islands. On the islands where single pairs are found the physical and vegetational aspects are the factors determining minimum space needs, and social intolerance should be of little or no importance. There is no chance to expand the area defended or utilized at the expense of other pairs.

The original dominant vegetation was composed primarily of red, white and jack pines (*Pinus resinosa*, *P. strobus* and *P. banksiana*), white spruce (*Picea glauca*), balsam-fir (*Abies balsamea*), white birch (*Betula papyrifera*) in the uplands and black spruce (*Picea mariana*), tamarack (*Larix laricina*), white cedar (*Thuja occidentalis*) and black ash (*Fraxinus nigra*) in the swamps and wet areas (Rosendahl, 1955). The present vegetation on most of the islands shows the effects of logging and burning, with aspen (*Populus tremuloides*) and white birch now being the principal dominants, although some of the islands retain remnants of the original pine forest.

METHODS

The islands used in this study vary from a small fraction of one acre to about 15 acres in extent. They were chosen on the basis of size, availability, and the ease with which reasonably accurate observations could be

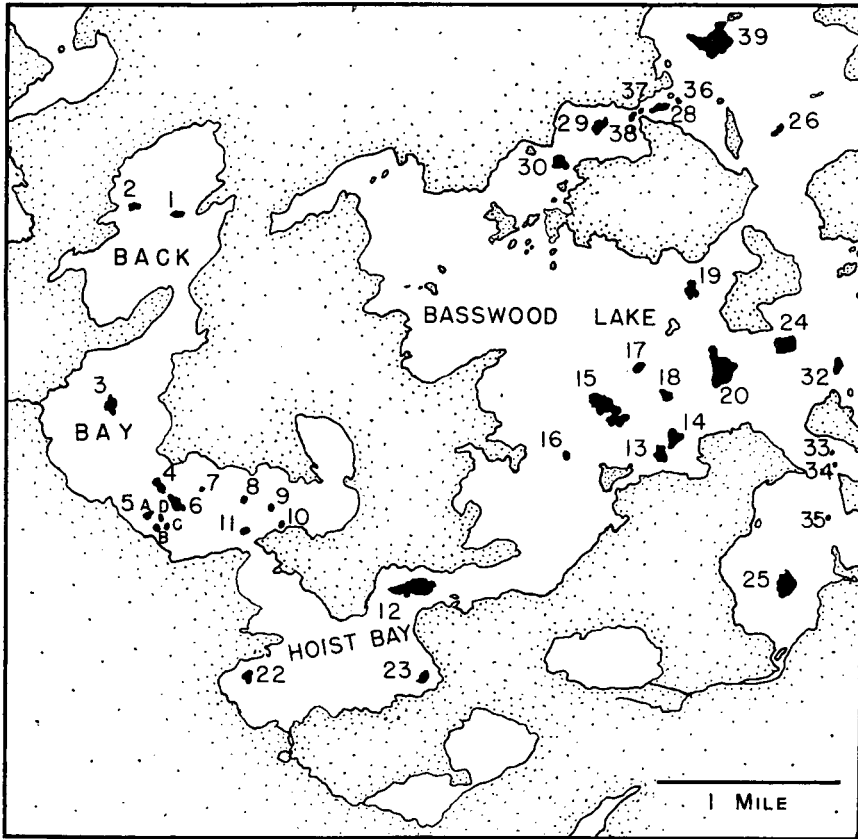


FIG. 1. Map of the Basswood Lake area, Minnesota. The islands on which bird populations were observed are blocked in and numbered.

made. The method of study was to make direct observations using sight and song records to determine the presence or absence of birds and to establish the number of pairs present. These observations were normally made early in the morning. Each island was visited on at least four different days during the breeding season. The maximum number of males found showing signs of stability (observed on two or more days and with behavior suggesting that they were in residence) was taken to be the number of nesting areas occupied. Rarely, verification of the presence of breeding birds was based on active nests even though the adults were neither heard nor seen. "Area per pair" as used here is based on dividing the area of the island (in acres) by the number of pairs present rather than extensive observations of the areas actually utilized or defended.

The Song Sparrow, Yellow Warbler, and Red-eyed Vireo were chosen for study because of their abundance and the ease with which observations could be made. They also normally obtain all of their requirements in a single continuous area. Each species utilizes a different level in the habitat and represents a different family of the Passeriformes.

FINDINGS

Song Sparrow. The Song Sparrow is a bird of the brushy edges which are found along the borders of forest openings and the lake shores. The preferred habitat here appears to be a grassy opening with a border of low brush and shrubs between it and the lake. Nesting, while normally on the ground, may take place in holes in trees or in small evergreens as much as seven feet off the ground where there are not suitable open areas.

It has been shown by Nice (1937) that during the breeding season this sparrow normally maintains and uses an area of between 0.7 and 1.5 acres. Nice (1943:152) stated that in central Ohio "the minimum size of a territory was some 2000 square meters (1/2 acre); an average size in a region well filled with Song Sparrows was some 2700 square meters (2/3 of an acre), while a few might include 6000 square meters (1 1/2 acres). During later years when the population was comparatively small, Song Sparrows might range over a larger region than when Interpont was filled to capacity." These figures represent very detailed observations of a mainland area.

The present study indicates that under the specialized conditions found on small islands the minimum territory size for Song Sparrows may be considerably less than that recorded for mainland areas. An examination of Table 1 shows that the minimum area may be as low as 0.04 acres, about one-tenth of the minimum size reported by Nice. This figure is for the small islands occupied by a single pair.

That the use of such a small area is of regular occurrence is borne out by the fact that island no. 8 had nesting birds for six consecutive years (see Table 1). In two of these years we observed second nests as well as fledglings. Island no. 33, which is also about 0.04 acres in size, had a nesting pair during one of the two years in which observations were made. The area may be nearly as small when two pairs are present, since the smallest average area per pair for two pairs was found to be 0.05 acres. However, this situation was unusual in that it involved a dominant and a definitely subordinate male. The dominant bird appeared at times to occupy all of the island while the subordinate bird was seen only on one half of the area except when being chased by the dominant male. Both males were observed to sing but the subordinate male's song was much weaker than that of his competitor and often was not carried to its normal completion. Repeated observations showed that both pairs were successfully

TABLE 1
NUMBERS OF BREEDING PAIRS OF SONG SPARROWS ON THE
ISLANDS IN BASSWOOD LAKE, MINNESOTA

Island No.	Pairs Observed						Greatest No. of pairs	Island area (acres)	Acres per pair
	1950	1951	1952	1953	1954	1955			
1	1	2	2	2	1	1	2	.33	.16
2	1	2	2	3	2	2	3	.9	.45
3	3	1	4	4	3	3	4	2.4	.60
4	1	1	1	3	1	2	3	2.6	.87
5A	1	1	1	3	1	2	3	1.2	.40
5B	1	0	0	1	0	1	.1	.10
5C	1	0	0	1	0	1	.2	.10
5D	1	0	0	1	1	1	.2	.20
6	4	1	2	0	0	4	4.0	1.0
7	1	0	0	0	0	1	1	.06	.06
8	1	1	1	1	1	1	1	.04	.04
9	1	1	2	1	1	2	.1	.05
10	1	1	1	1	2	1	2	.2	.10
11	1	0	0	1	1	1	1	.1	.10
12	1	5	5	5	9.3	1.96
13	1	1	2	2	2	2.3	1.15
14	1	1	3	1	3	4.1	1.4
15	1	1	11.6	11.6
16	1	1	1	1	0	1	.08	.08
17	1	2	2	2	2	.35	.17
18	2	1	1	3	1	2	3	.9	.30
19	1	1	3.5	3.5
20	1	1	11.6	11.6
22	2	2	2	1.4	.70
23	1	2	2	2	3.1	1.55
24	1	1	5.9	5.9
25	5	4	5	6.1	1.2
26	1	5	5	1.6	.52
28	1	1	1.8	1.8
29	0	0	2.4
30	0	0	2.7
32	0	0	2.8
33	1	0	1	.04	.04
34	1	1	.05	.05
35	0	0	.06
36	1	1	.5	.5
37	1	1	1.7	1.7
38	0	0	1.0
39	0	0	18.6

raising young. The next smallest area observed to have two pairs was an island of 0.2 acres, about twice the size of that discussed above. This island was cigar shaped, which undoubtedly helped to maintain a state of stability. When three pairs of Song Sparrows were present the smallest average area occupied per pair was about 0.3 acres. Minimum areas per pair of 0.6 and 0.5 acres were observed when four and five pairs were present. These last figures are not appreciably different from the minimum-sized areas of one-half acre reported by Nice (1943:152).

TABLE 2
NUMBERS OF BREEDING PAIRS OF YELLOW WARBLERS ON THE
ISLANDS IN BASSWOOD LAKE, MINNESOTA

Island No.	Pairs Observed						Greatest No. of pairs	Island area (acres)	Acres per pair
	1950	1951	1952	1953	1954	1955			
1	1	2	0	1	1	0	2	.33	.16
2	2	1	1	3	2	1	3	.9	.3
3	1	0	3	3	2.4	.8
4	1	1	0	1	2.6	2.6
5A	1	1	1	1	1.2	1.2
5B	0	0	0	.1
5C	0	0	0	0	.1
5D	0	0	0	0	.2
6	1	0	1	4.0	4.0
7	0	0	0	0	0	.06
8	0	0	0	0	0	0	0	.04
9	1	0	1	1	1	.1	.1
10	0	1	1	1	.2	.2
11	0	1	1	.1	.1
12	1	3	3	3	9.3	3.1
13	1	1	0	0	1	1	2.3	2.3
14	2	0	2	4.1	2.0
15	4	4	11.6	2.9
16	1	0	1	1	1	.08	.08
17	0	0	0	0	.35
18	1	1	2	2	2	.9	.5
22	1	1	1	1.4	1.4
23	0	0	0	3.1
24	1	5	5	5.9	1.2
25	4	4	6.1	1.5
26	5	5	1.6	.3
28	1	1	1.8	1.8
29	0	0	2.4
30	0	0	2.7
32	0	0	2.8
33	0	0	0	.04
34	0	0	.05
35	0	0	.06
36	1	1	.5	.5
37	2	2	1.7	.8
38	0	0	1.0
39	0	0	18.6

Yellow Warbler. The Yellow Warbler is a bird of the brushlands, preferring to nest and to do much of its feeding in underbrush and low trees, especially where an edge is present. Kendeigh (1941:171) has suggested that the average size of Yellow Warbler territories is about 0.4 acres. However, the area studied by him in Iowa apparently lacked adequate feeding grounds, since the birds regularly left their territories in thickets of *Cephalanthus* to feed in the forest nearby. Some flew as far as 1200 feet to feed. We have no observations of Yellow Warblers leaving one of the islands to feed, although the less common Myrtle Warbler (*Dendroica coronata*) was observed to do so frequently. The map drawn by Kendeigh (1941)

shows that there is considerable variation in territory size but he did not give values for the maximum or minimum area. Differences in the two habitats make it difficult to compare the results of the two studies.

The smallest island observed to be occupied by a single pair of Yellow Warblers was about 0.08 acres in extent (see Table 2). Islands with two breeding pairs were not smaller than .33 acres, which allowed about 0.16 acres per pair. This is twice the minimum area per pair where only one pair was observed. For three or more pairs a minimum area of 0.3 acres each was observed. This figure agrees very well with the average figure given by Kendeigh (1941) but is three times as large as our minimum figure.

Red-Eyed Vireo. The habitat which the Red-eyed Vireo seems to favor is a broadleaved woodland with an undergrowth of brush and slender saplings. This situation gives the vireo a nesting site in the low undergrowth and a feeding area in the aspen and birch overstory. Lawrence (1953) and Kendeigh (1947:55-57) have shown that the space utilized by the Red-eyed Vireos on their study areas varied from 0.7 to 2.6 acres.

Singing males were observed on islands in Basswood Lake with areas as small as 0.08 acres. Although nests were not found, apparently-resident males were observed in two of the four years that we examined this island (island no. 16; see Table 3).

The smallest island upon which a Red-eyed Vireo's nest was found was island no. 1 which is 0.33 acres in extent. The smallest area per pair when two pairs were present was 0.4 acres. Nesting was not observed, although the singing males were observed consistently on the same song perches. When three pairs were present the smallest area per pair was 0.3 acres. An average area of 1.4 acres was available per pair when all three pairs were observed nesting. When four or five pairs were present the average available area was considerably larger—about 2.3 acres.

The smallest area observed when a single pair was present was about one-tenth the minimum observed on the mainland by Lawrence (1953) and Kendeigh (1947). When nesting was observed the smallest area was about 0.4 acres or about one-half the minimum observed by Kendeigh (1947) and Lawrence (1953). The average area available when four or five pairs were present approached the maximum figure of 2.6 acres determined by these workers. Of course some of the available area may not have been used, so that these figures may be larger than the areas actually utilized.

DISCUSSION

The figures given on the space required, utilized, or available are averages of the number of pairs present divided into the area involved. Thus in some cases the actual minimum area may be considerably smaller than the one listed as used. Time limitations often made thorough search for nests

TABLE 3
NUMBERS OF BREEDING PAIRS OF RED-EYED VIREOS ON THE
ISLANDS IN BASSWOOD LAKE, MINNESOTA

Island No.	Pairs Observed						Greatest No. of pairs	Island area (acres)	Acres per pair
	1950	1951	1952	1953	1954	1955			
1	1	0	1	1	0	0	1	.33	.33
2	1	1	1	3	1	2	3	.9	.3
3	1	1	1	1	0	1	1	2.4	2.4
4	1	1	1	1	1	2.6	2.6
5A	1	0	0	1	1	1.2	1.2
5B	1	0	0	1	.1	.1
5C	0	0	0	0	.1
5D	0	0	0	0	.2
6	1	1	1	1	4.0	4.0
7	0	0	0	0	0	0	0	.06
8	0	0	0	0	0	0	0	.04
9	0	0	0	.1
10	1	0	0	1	.2	.2
11	1	0	0	1	.1	.1
12	1	3	4	4	9.3	2.3
13	1	1	0	0	1	2.3	2.3
14	0	1	3	1	3	4.1	1.4
15	2	5	5	11.6	2.3
16	0	1	1	0	1	.08	.08
17	0	0	0	0	.35
18	1	2	1	2	.9	.4
19	1	1	3.5	3.5
20	1	1	11.6	11.6
22	0	0	0	1.4
23	0	0	0	3.1
24	3	3	5.9	2.0
25	1	2	2	6.1	3.0
26	0	0	1.6
28	0	0	1.8
29	0	0	2.4
30	0	0	2.7
32	0	0	2.8
33	0	0	0	.04
34	0	0	.05
35	0	0	.06
36	0	0	.5
37	0	0	1.7
38	0	0	1.0
39	4	4	18.6	4.6

impossible. No attempt was made to follow fledglings through to a stage of independence. Fledging is here considered to indicate that the area was adequate for the raising of young. However, some detailed data are available for some of the Song Sparrows found on the very small islands.

In the previous discussion it was shown that Song Sparrows which inhabit islands will utilize areas as small as one-tenth the minimum size defended by birds on the mainland and in contact with others of their own species. The Red-eyed Vireo was found on very small areas but the smallest island

TABLE 4
MINIMUM AREA IN ACRES PER PAIR AT DIFFERENT POPULATION LEVELS

No. of Pairs	Song Sparrow		Yellow Warbler		Red-eyed Vireo	
	All Observations	Nesting Observed	All Observations	Nesting Observed	All Observations	Nesting Observed
1	0.04	0.04	0.08	0.1	0.08	0.33
2	0.05	0.05	0.16	0.16	0.4
3	0.30	0.30	0.30	.30	0.3	1.4
4	0.60	0.60	1.5	2.3	2.3
5	0.52	1.20	0.3	.30	2.3	2.3

on which breeding was ascertained was about 0.33 acres. This is about one-half the minimum-sized area reported by Lawrence (1953) for mainland areas. On the other hand the smallest area utilized by the Yellow Warbler was 0.08 acres which is only about one-fifth the average of 0.4 acres given by Kendeigh (1941). However, this area is probably not much different than the minimum found by him.

In all three species the minimum area utilized increased with the number of pairs present until three to five pairs were present (Table 4). These values then were approximately the same as those reported from the mainland by other authors. We observed no cases of birds nesting on one island and feeding on (or including as part of their territories) parts of other islands or the mainland.

Many reasons for the spacing of pairs have been postulated. These include:

- (1) it is necessary to have a certain amount of conflict in order to synchronize breeding;
- (2) it ensures an adequate food supply for the young;
- (3) it prevents the undue increase of the species;
- (4) it offers protection from interference in the orderly sequence of the nesting cycle.

The first hypothesis, which suggests that it is necessary to have conflict in order to synchronize breeding within the population, appears to be quite workable with colonial sea birds but less so with non-colonial passerines. In the three species observed, the single pairs on small islands removed from direct contact with others of their own species appeared to be as successful as those nesting where there was considerable direct contact with their neighbors. There was of course a certain amount of indirect contact in that singing birds can be heard for considerable distances over the open water. This is especially true for the Red-eyed Vireo. However, it is difficult to see how this factor can be important with these species.

It has long been claimed that many birds limit their own breeding densities through territorial behavior, and thereby insure a food supply for themselves and their young. While the idea superficially is attractive, there is little

positive evidence in its favor. The data presented earlier suggest that the size of the territory normally chosen by these three species on mainland areas is not determined by the food supply. In the case of Song Sparrows, island areas may be as little as one-tenth of the minimum area utilized on the mainland. These islands often appear to be quite sterile and it is difficult to visualize their approaching the production of food per unit area characteristic of the area studied by Nice (1937; 1943) in central Ohio. Observations of Song Sparrows on island no. 8 have shown that this area is large enough to serve this purpose. Although it is but 0.04 acres in extent, at least one brood has been fledged there in each of the six years in which observations were made. In one year two broods were known to have been raised. This island is so well isolated that feeding is definitely limited to its surface. The data for the Red-eyed Vireo and Yellow Warbler are similar but not so well defined.

If the food supplies were the all-important factor and the territories were defended on this basis, the minimum area occupied as demonstrated on the islands should be about the same as the minimum area defended and utilized on the larger islands and on the mainland.

The third theory suggesting "that it prevents undue increase of the species" does not seem tenable because most species tend to fill all the vacant areas available. Predation, accident and other extrinsic causes normally eliminate any surplus birds.

The last suggestion that a territory offers protection from interference in the orderly sequence of the nesting cycle seems to be the nearest the truth. This of course covers many factors and actually only suggests that a territory during the breeding season helps the species reproduce itself. Mayr (1935) considered that pairing and mating functions are at the root of territorial behavior. This allows for the best utilization of the area by reproducing birds with the possibility of many factors being involved.

CONCLUSIONS

The data gathered indicate that in some birds the minimum amount of space used by a pair to raise their young successfully may be much smaller when the boundaries are strictly physical barriers rather than invisible lines determined by intraspecific conflict. The three species observed reacted similarly to the situation of reduced space. The Song Sparrow on occasion successfully utilized islands less than one-tenth the size of the minimum area reportedly required on the mainland. The Red-eyed Vireo and the Yellow Warbler showed similar but less pronounced tendencies. The size of a territory is based upon a number of factors and not on single factors such as food.

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