FOOD HABITS AND AVAILABLE FOOD OF OVENBIRDS IN RELATION TO TERRITORY SIZE

BY JUDITH STENGER

THE greatest controversy among those studying territorial behavior concerns the end for which territories are established by birds (Nice, 1941). A food value theory postulates that the function of territorial behavior is to space out pairs of birds over an area to ensure an adequate supply of food for the successful rearing of the young. This implies that the territory size is related to the amount of food available to the birds within their territories. In this study the relation between territory size and available food was investigated for the Ovenbird (*Seiurus aurocapillus*).

The Ovenbird gathers invertebrate food from the surface of the litter on the forest floor. The feeding ground thus consists of an area, rather than a volume, of the forest. A study of the food habits of the Ovenbird was undertaken by a) examination of stomach contents, and b) sampling of the food items in the places where the Ovenbird normally feeds. Information from these sources was compared to determine whether or not the Ovenbird selected specific items of food. Knowing this, the amount of food available in each territory could be estimated and compared to the size of the territory.

Changes in the amount of invertebrate food present on the forest floor throughout the breeding season of the Ovenbird were determined with a view to learning their relation to the stages of the breeding cycle.

The study was carried out in Algonquin Park, Ontario, at the Wildlife Research Station of the Ontario Department of Lands and Forests during the summers of 1955 and 1956.

FOOD HABITS

Observations on the Ovenbirds revealed that most of the food was taken from the leaf litter on the forest floor. The food items were picked up with the bill as the birds walked along the ground. Ovenbirds do not scratch in the litter, but may occasionally turn over a leaf with the bill. Some invertebrates were picked up from the low ground vegetation or from the sides of decaying logs. Only once was an Ovenbird observed attempting to feed in a tree; in this activity the bird was extremely awkward. This observation was made during a two-week period at the end of June when the striped maple worm was particularly abundant in maple forests.

Except for some very open areas within the territories of a few of the birds, the areas in which the Ovenbirds fed were evenly distributed throughout the territory. Where such non-utilized areas occurred within the territories they were subtracted in the consideration of feeding area. Density of brush or ground vegetation had little bearing on the distribution of feeding activity. Thus it was possible to equate the territory with the feeding area.

The more exact food habits of the Ovenbird were determined by examining the contents of 98 stomachs. Forty of these were collected in Algonquin Park during August and September of 1955 in forests similar to the study areas. An additional 24 birds were collected in the same area during June, July and early August of 1956. The remaining 34 stomachs, taken over 11 years, were made available by the Research Division of the Ontario Department of Lands and Forests. Most of these came from various points in central Ontario.

The invertebrates eaten by the Ovenbirds were identified by the author and the numbers of each kind listed. From these numbers and from the average weights of field-collected specimens of the same invertebrate types (calculated on the basis of 12–50 specimens of each) the percentages by weight of each food item in the stomachs was calculated. Percentages were calculated from the combined stomach analysis data, since there was too much variation when such percentages were calculated for each stomach individually. No allowance was made for differential rates of digestion for the different food items.

The stomach analyses (Table 1) indicate that the diet is not the same from year to year, and for this reason the data are given separately for the years 1955 and 1956. Results for the stomachs that were collected over a period of 11 years are combined. Data for the stomachs of five nestlings collected in 1956 are not combined with the data for the adults but are listed separately. The data were analyzed on a seasonal basis also, but it was found that the numbers of stomachs collected each month of the breeding season in each year were too few to show statistically significant differences in the food items eaten during the season.

The food items found in the stomachs can be classified according to their vertical distribution in the forest (Table 2). The category for the surface and subsurface forms includes those which occur exclusively on the ground and therefore represents the minimum food gathered from the forest floor. The value for this category would probably be much higher if forms that occur on the ground only occasionally were included. Also the "widespread" group contains a high proportion of forms that occur on the ground. If it is kept in mind that the forms listed as "surface or subsurface" represent a minimum, it can be seen from Table 2 that most of the food is gathered from the forest floor.

TABLE 1

STOMACH ANALYSES

Percentage by weight formed by each invertebrate group in the diet

Invertebrate group	*11 yrs. adults*	*1955 adults*	*1956 adults*	*1956 nestlings*
Otiorhynchinae	19.9%	18.6%	4.4%	
Carabidae	20.7	14.4	11.3	15.4%
Staphylinidae	.6	.5	.3	
Miscellaneous Coleoptera	4.4		7.0	
Unidentified Coleoptera	20.7	11.3	10.6	10.8
Coleoptera larvae	1.6	4.2	1.7	
Lepidoptera larvae	2.9	10.8	32.9	35.4
Diptera larvae		.6	2.0	6.1
Unidentified larvae	24.0	7.5	10.7	17.3
Gasteropoda	2.2	1.6	3.9	12.3
Diplopoda	.9	1.9	1.7	
Chilopoda			.5	
Formicidae	12.3	21.3	4.1	
Miscellaneous Hymenoptera	1.7	1.3	.8	
Diptera	.3	.8	.6	1.5
Hemiptera	1.7	.8	.8	1.5
Araneida	6.1	2.6	4.7	3.1
Lepidoptera and Diptera pupae		1.6	2.0	
Lepidoptera adults				9.2

TABLE 2

PERCENTAGES BY WEIGHT OF THE DIET MADE UP OF INVERTEBRATES GROUPED ACCORDING TO THEIR VERTICAL DISTRIBUTION IN THE FOREST

	11 years	*1955*	*1956*
Surface and subsurface forms	83.3%	76.0%	49.5%
Vegetation forms	1.7%	.8%	.8%
Widespread forms	15.0%	23.0%	49.4%

Thus only the forest floor was considered in the study of the amount of food available to the Ovenbird.

Insect larvae, adult Coleoptera, and Gasteropoda are the most important constituents of the nestling diet. The diet does not differ greatly from that of the adults except in the proportion of the larvae, which make up a greater proportion of the nestling diet (Table 1). In 1955 several young birds were collected a few days after they had left the nest and their diet did not differ from that of the adults.

LITTER ANALYSIS

During the summer of 1956 two methods were employed to extract invertebrates from samples of litter collected from the forest floor: 1)

Heat-light extraction with a Berlese funnel; 2) Simple screening technique.

The Berlese funnel used in this study was modelled after a funnel used by MacFadyen (1955). When a 150-watt bulb was used as the source of heat and light, those invertebrates that are of the size that the Ovenbird eats come out in about two days. This time limit was adopted for purposes of uniformity. Early in the summer, however, samples were frequently abnormally wet and some were kept in the funnels three to four days. By this method 105 samples were processed.

By the screening technique, the litter samples were shaken through a series of screens and all the invertebrates were collected from the screenings. One hundred and thirty-six samples were processed.

The size of the samples used for both these methods was one square foot of litter from the forest floor. The depth of the samples included the low vegetation covering the square foot and the loose leaves down to the layer where decomposition occurred. The samples were taken at the approximate centre of each 66-foot square (size of grid used in territory study) within the territories in a spot representative of the ground cover of the grid square. "Berlese" and "screening" samples were distributed randomly with respect to each other and approximately equal numbers were extracted by each method for each territory. About 16 to 20 samples were collected from each territory depending on the size of the territory and the uniformity of the structure of the forest.

The two extraction methods were not equally efficient for all the invertebrate groups. The differences in efficiency can be explained by the mechanical procedures involved in the two methods. Stationary forms such as the pupae are not expected to appear in the "Berlese" samples except when they fall through the sieve accidentally. Many Gasteropoda can also probably be considered with the stationary forms because they do not move quickly enough to escape dessication in the funnel.

To determine the composition of the forest floor fauna, results of 105 samples extracted by each method (210 altogether) were combined using the following adjustments. For those invertebrates where there was no significant difference in extraction efficiency, the two totals were added. For the forms that were obtained with the greatest efficiency by the "Berlese" method, the "Berlese" values were doubled except for the winged photo-positive forms (Diptera and Lepidoptera) which may have flown into the aperture of the funnel. For these the "screening" values were doubled. For those that were obtained with the greatest efficiency by the "screening" method, the "screening" values

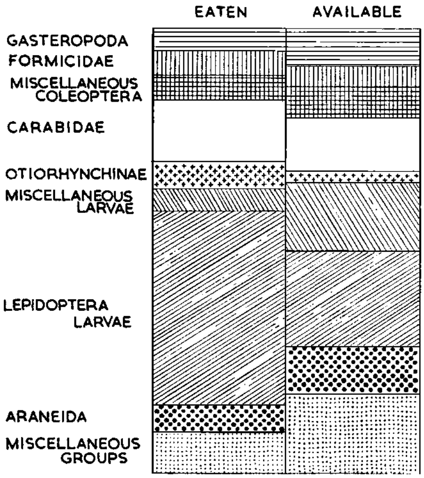

FIGURE 1. Comparison of percentages of invertebrate groups in the diet with the percentages of the same groups in the litter samples (available on forest floor). Unidentified Coleoptera and unidentified larvae were excluded in the calculation of percentages for the diet.

were doubled (Table 2). The adjustments give an approximate model for the number of invertebrates present in 210 samples. From these numbers the percentage by weight for each invertebrate group is calculated.

COMPARISON OF FOOD EATEN AND FOOD AVAILABLE

The invertebrate groups eaten by the Ovenbird (Table 1) were compared with the invertebrates found in the litter samples (Table 3) to determine whether they were eaten in the approximate proportions in which they were available. The Annelida, Phalangida, and adult Lepidoptera were not compared because of their rarity in the stomachs and litter samples; i.e., the sample of stomachs and litter samples was not large enough to compare the weights of these items in them. Only the 1956 data for stomachs and samples are compared since the diet varies slightly from year to year.

All the invertebrate groups found in the stomach analyses were also found in the litter samples from the forest floor. The percentages made up by the various invertebrate food items in the diet and the litter samples cannot be compared directly because the percentage of each item in both the diet and the litter is not independent of the percentages made up by the other items. Certain conclusions can be drawn when the percentages of the invertebrates eaten (those forming more than five per cent of the diet) and the percentages of invertebrates found in the litter are compared graphically (Figure 1).

From Figure 1 it becomes apparent that the major items in both the diet and the litter occur in similar proportions (Carabidae, Otiorhynchinae, miscellaneous Coleoptera, Gasteropoda, Formicidae). Lepidoptera larvae occur in greater proportion in the diet than in the litter, indicating that some larvae may have been gathered from trees, that

TABLE 3

THE NUMBERS,[1] CALCULATED WEIGHTS, AND PERCENTAGES BY WEIGHT (GMS) OF THE TOTAL FOR THE DIFFERENT INVERTEBRATE GROUPS[2] IN 210 LITTER SAMPLES FOR 1956

Invertebrate group	*Number*	*Calculated weight*	*Percentage of total*
Otiorhynchinae	59	.579	2.7
Carabidae	102	2.550	11.8
Staphylinidae	70	.322	1.5
Miscellaneous Coleoptera	114	1.163	5.4
Coleoptera larvae	244	1.854	8.6
Lepidoptera larvae	345	4.589	21.3
Diptera larvae	112	1.467	6.8
Gasteropoda	310	1.798	8.3
Diplopoda	218	1.657	7.7
Chilopoda	390	.858	4.0
Formicidae	620	1.178	5.5
Miscellaneous Hymenoptera	22	.042	.2
Diptera	78	.062	.3
Hemiptera	127	.165	.8
Small Araneida	1142	1.028	4.8
Medium Araneida	183	1.263	5.9
Lepidoptera and Diptera pupae	76	.980	4.5

[1] Numbers adjusted as outlined on pages 338-339.
[2] Only invertebrates eaten by Ovenbirds are included.

there is selectivity for the larvae, or that an increased number of larvae occur on the ground during the short period of greatest abundance. For this period some stomach samples are available, but no litter sampling was done to determine whether the greater number of larvae found in the stomachs could have been obtained from the litter.

Among the remaining groups are some that do not occur in the same proportions in the diet as they do in the litter (Figure 1). These are the Coleoptera and Diptera larvae (miscellaneous larvae), Diplopoda, Chilopoda, Staphylinidae, Lepidoptera and Diptera pupae (miscellaneous groups). These forms all have in common that they are subsurface forms and do not usually come to the top of the litter as do the other forms. Thus they are probably not as available to the Ovenbird as the litter samples would indicate, since Ovenbirds do not scratch in the litter, although they may occasionally turn over a leaf with the bill.

It can be concluded that in general there is no selectivity for preferable items on the forest floor by the Ovenbirds and that most invertebrate groups are eaten in numbers approximately proportional to their availability.

The diet varies from year to year, as does also the available food. A greater percentage of the diet was made up of Coleoptera in 1955 (Table 1), corresponding to a greater number present in the litter. On the other hand, insect larvae showed up in much higher percentage in the diet in 1956 than in 1955 (Table 1), corresponding to a higher percentage present on the forest floor in 1956. This is further evidence that the food is eaten in the approximate proportions in which it is available to the birds.

EXTENT OF TERRITORIES

Territories are established by male Ovenbirds in early May before the arrival of the females. The female takes no part in defense of the territory but restricts her activities within the boundary of the male territory. In his extensive work on this species, Hann (1937) found that the male takes no part in building the nest (time required—five days) or incubating the eggs (about 12 days), but actively participates in feeding the young during the nestling stage (about 8 days). Hann reported that the chicks (usually 5) after leaving the nest become divided between the male and female, the female taking her charges out of the territory permanently, while the male and his chicks remain within the territory until the chicks are independent. Our observations supported these conclusions.

Territories held by 13 males in 1956 and those held by nine males in 1955 were studied in four forest habitats. The total utilized territory, as well as changes in the area utilized daily throughout the breeding season, was investigated. Sight and song observations were plotted on maps of the study areas, which were surveyed into 66 ft. grids. Data from all observation periods were combined and the central 95 per cent of the observation points was enclosed by straight lines to give a total utilized territory for the breeding season. Points for first and second nesting attempts were considered separately. A few of the territories had open, unforested areas within them which were not utilized by the birds and these were subtracted from the polygons outlined by straight lines. Areas utilized daily were obtained by a modification of the observation-area curve method (Odum and Kuenzler, 1955) and will be described in another paper.

Average total utilized territory differed in the four forest habitats in 1956 as follows: mature maple, 3.2 acres (2 males); mixed maple-birch-conifer, 2.4 acres (3 males); pine-birch, 2.2 acres (3 males); aspen, 1.8 acres (3 males). Total utilized territory sizes for individual males are listed in Table 4. Feeding observations were evenly distributed within the total utilized territories. There is usually a buffer zone between the total utilized territories of neighboring birds, although this may not occur between some individuals. Most of the points (five per cent) rejected in the estimation of the total utilized territory occurred in the buffer zone, where there was a noticeable decrease in aggressiveness.

Changes in area utilized daily are as follows. The area utilized was large during the premating period before the females arrived and during a short mating period which preceded nest-building activities. During nest-building and egg-laying periods the area utilized shrank considerably. This was followed by an increase during incubation to a size approximately that utilized during the premating period. Area utilized during the nestling period apparently was as large as during the incubation period, while that utilized after the young left the nest differed for different individuals.

Invertebrate Food Available Within the Territories

If territory functions to provide an adequate supply of food for the birds, it might be expected that territory size is inversely proportional to the density of food items within the territory.

To obtain a measure of the amount of food available on the forest floor in each territory, those invertebrate types which also appear in the diet were weighed for each litter sample. There was no significant difference between the average weight of invertebrates per sample obtained by the two extraction methods. Thus the weights obtained by the two extraction methods were considered comparable.

In calculating the weight of invertebrate food per sample for the territories, some of the invertebrates were not included in the weights. Chilopoda and Diplopoda were excluded because only a small proportion of them were eaten, their absence in the diet being explained by their habit of avoiding the surface of the litter. Also excluded are the Annelida, Phalangida, and adult Lepidoptera because, as outlined previously, these forms are rare and the number of litter samples completed was not large enough to give an adequate picture of the role they play in the amount of available food.

The total size of the territories, the forest type in which they occurred, and the average weight of invertebrates per sample in each total

TABLE 4

SIZE IN ACRES AND THE AVERAGE WEIGHT OF AVAILABLE FOOD PER SAMPLE FOR EACH TERRITORY IN 1956

Forest type	*Bird*	*Average Food/sample (gms)*	*Total territory size (acres)* *1st nesting*	*Renesting*
Aspen	M28	.106	1.5	1.1
Aspen	M26	.091	1.9	
Aspen	M27	.088	2.1	
Conifer-birch	M24	.074	2.1	
Conifer-birch	M20	.075	2.2	
Conifer-birch	M23	.059	2.2	
Mixed	M32	.066	1.5[1]	3.4
Mixed	M7	.074	1.8[2]	
Mixed	M31	.066	2.2	
Mixed	M3	.072	2.4	
Mixed	M5	.060	2.7	3.6
Maple	M30	.072	2.5	
Maple	M29	.043	4.0	

[1] First nesting attempt includes only two days' observation.
[2] Unmated.

territory are listed in Table 4. From Table 4 it can be seen that there is a relation between the available food and the total territory size, which holds within one forest type as well as among the four forest types (aspen, conifer-birch, mixed, maple). Of particular interest are the territories of M30 and M29, both of which were in mature maple forest. These two territories showed the greatest similarity in structural aspect of the forest, and yet showed a very marked difference in the size of the total territory established, as well as the amount of invertebrate food present.

A correlation of .82 is obtained when ρ is calculated by Spearman's rank method (Snedecor, 1956) for total territory size and the weight of invertebrate food present. These data suggest that the territory established may be directly adjusted in size to the amount of food present.

Other studies in collaboration with Dr. J. B. Falls showed that territory size increased as canopy density increased and as the density of ground vegetation decreased. Abundance of ground vegetation is usually indicative of the amount of humus of a non-acid type. The development of such a humus is dependent on the nature of the leaves which comprise the litter and ultimately on the species comprising the canopy. The development of a deep non-acid humus is conducive to invertebrate abundance and thus these factors are probably all interrelated.

TABLE 5

AVERAGE WEIGHT OF INVERTEBRATES PER SAMPLE FOR THE MONTHS IN THE BREEDING CYCLE

Month	*Average weight per sample (gms)*
May 17–31	.074 (14 samples)
June	.074 (31 samples)
July 1–15	.106 (15 samples)
July 16–31	.061 (24 samples)
August 1–10	.066 (20 samples)

The maximum weight of invertebrates occurred during the first half of July (Table 5). This was an increase over the average for May of about 40 per cent. The eggs in most Ovenbird nests hatched on June 26, 27, or 28. Thus the maximum weight of invertebrates occurs at approximately the same time as the nestling period, when the demand for food in the territory is greatest.

DISCUSSION

The "territory" of the Ovenbird can be represented as an area of utilization which varies in size and shifts slightly from day to day. The combined areas of each daily territory represent the total utilized territory. The area utilized varies from day to day during the breeding season, but appears to have no relation to the number of birds in the family unit obtaining food from it. Thus when the amount of food available is compared to territory size an attempt must be made to interpret the biological meaning of such a relation.

If territory is to ensure an adequate supply of food for the successful rearing of the young, some mechanism must be at work when territories are first established, such that territory will be sufficiently large to supply the extra food required when the eggs hatch since the size of the area utilized does not increase at hatching.

One of Hinde's (1956) arguments against the food value theory is the fact that territories are not defended against other species with similar food requirements. For the Ovenbird, observations showed that the feeding ecology has very little overlap with other species in Algonquin Park. The other common ground-feeding species is the White-throated Sparrow (*Zonotrichia albicollis*), which can be found in the same habitats as the Ovenbird. Aside from the fact that it probably has a very much higher proportion of seeds in the diet, it also differs markedly in its feeding activity from the Ovenbird. Its feeding is much more localized; i.e., it remains in one spot for longer periods of time and scratches to the deeper layers of the litter. Thus the food niche of the

White-throated Sparrow is probably quite different from that of the Ovenbird, and the question of interspecific competition does not arise between the two.

Further, the fact that no expansion of the territory occurs during the nestling stage is probably highly significant. The periods of the breeding cycle are usually well synchronized for all the birds in one area. Thus if an expansion during the nestling period did take place, it would lead to a great deal of struggling among the males of this species when their important duty is to feed the young, since all birds would be trying to expand their territories at the same time.

The behavior of the male, who assists in feeding the young, changes markedly when the eggs hatch. He no longer sings for prolonged periods and the lack of song makes him seem very secretive. The area utilized is as large as during premating and incubation when he is involved in display. Presumably this area is used for the procurement of food for the nestlings.

Usually birds spend more time gathering food during the nestling stage (Palmgren, 1949 from Kuusisto, 1941). In addition to increased time spent by the Ovenbirds in gathering food, there is an increase in the weight of invertebrates on the forest floor from May to July, such that a maximum occurs coincidentally with the nesting period. The increase in the weight of the invertebrates on the forest floor is probably even greater than apparent from the data. During the last two weeks of May, as opposed to the first two weeks of July, the temperature during the night often went down to freezing or below, thus rendering many invertebrates inactive and keeping them below the surface during the early hours of the morning when the birds were engaged in their feeding activities. Thus, during July, when nestlings are being fed, more invertebrates would be active at the surface for a longer period of time each day than during May when the territories are first established. Lack (1950) put forward the view that the breeding season of each species of bird is adjusted by natural selection to that season of the year when the food that the bird is adapted to collecting is sufficiently abundant for it to raise a family. This postulate is borne out by the Ovenbird; but whether this phenomenon is the sole mechanism providing adequate food or whether the territory provides an excess of food throughout the season still requires to be answered.

SUMMARY

From examination of stomach contents, the food of the Ovenbird was found to consist chiefly of invertebrates gathered from the forest floor. These invertebrates are not taken selectively but are eaten in the approximate proportions in which they are available.

The weight of invertebrates per litter sample within the territory varied inversely with the size of the total territory established during the breeding season. This correlation held within habitats, as well as among habitats.

The weight of invertebrate food on the forest floor increased during the breeding season to reach a peak during the first two weeks of July, which corresponded with the nestling period of the Ovenbird chicks.

ACKNOWLEDGEMENTS

The manuscript is based on part of an M.A. thesis presented at the University of Toronto. The field work was carried out at the Wildlife Research Station of the Ontario Department of Lands and Forests in Algonquin Provincial Park during the summers of 1955 and 1956. The author is very much indebted to Dr. C. D. Fowle and Mr. R. O. Stanfield for so generously making these facilities available. It is a pleasure to acknowledge the constant encouragement and advice of Dr. G. F. Bennett, who suggested the problem, Dr. L. Butler, who made helpful suggestions for the statistical analysis of the data, and Dr. J. B. Falls for reading and discussing the manuscript. The project was supported by funds granted to Dr. J. B. Falls by the National Research Council of Canada and by the Ramsay Wright Scholarship awarded to the author by the University of Toronto.

LITERATURE CITED

HANN, W. H. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull., **49**: 145–237.

HINDE, R. A. 1956. Territories of birds. Ibis, **98**(3) : 340–369.

LACK, D. 1950. The breeding seasons of European birds. Ibis, **92**: 288–316.

MACFADYEN, A. 1955. Methods for extracting soil arthropods. Soil Zoology, Butterworth's Scientific Publications, London.

NICE, M. M. 1941. The role of territory in bird life. Am. Mid. Nat., **26**(3) : 441–487.

ODUM, E. P. and E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk, **72**(2) : 128–138.

PALMGREN, P. 1949. On the diurnal rhythm in birds. Ibis, **91**: 561–576.

SNEDECOR, G. W. 1956. Statistical methods. Iowa State College Press, Ames, Iowa.

Department of Zoology, University of British Columbia, Vancouver, B. C.

WESTERN GREBES ESCAPING OVERLAND FROM A SMALL POND ON ISLE OF BAYS TO OLD WIVES LAKE, SASKATCHEWAN, AUGUST 8, 1956. *Photo by F. W. Lahrman.*