5-1967

Feeding Ecology and Territorial Behavior of the Yellow Warbler

Merrill J. Frydendall
Utah State University

FEEDING ECOLOGY AND TERRITORIAL BEHAVIOR OF THE YELLOW WARBLER

by

Merrill J. Frydendall

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Zoology

UTAH STATE UNIVERSITY
Logan, Utah

1967

ACKNOWLEDGMENTS

I wish to acknowledge the guidance and assistance of Dr. Keith L. Dixon throughout the course of this study. Valuable criticisms offered by Drs. D. M. Hammond, F. H. Wagner, H. H. Wiebe, and Mr. W. J. Hanson have been beneficial in the final preparation of the dissertation.

Appreciation also goes to members of the entomology department, especially to W. J. Hanson for his aid in insect identification, S. Kohler for his help in identification of stomach contents, and C. Summers and L. B. Coons for aid in the insecticide application.

My final and deepest appreciation goes to my family for their patience and understanding, and especially to my wife, Karen, for her help typing the manuscript and field notes, along with her many other duties.

This study was supported in part by Public Health Service Fellowships 1-F1-GM-28,401-01 and 1-F1-GM-28,401-02 from the National Institutes of Health and a National Science Foundation Grant G-23904 to Dr. Keith L. Dixon.

Merrill J. Frydendall

TABLE OF CONTENTS

LIST OF TABLES

Table | Page

LIST OF FIGURES

Figure | Page

INTRODUCTION

A controversy dating from the appearance of Altum's book, Der Vogel und sein Leben, 1868 (Mayr, 1935) is that of the biological function or functions of the territorial behavior in birds. However, attention was not focused upon this problem until the advent of Howard's book, Territory in Bird Life, published in 1920. In a general review of the problem Hinde (1956) discussed several functions of the territory and presented evidence both for and against their importance. The more important of these presumed functions are: (1) limitation of population density; (2) facilitation of pair formation and maintenance of the pair bond; (3) reduction in interference with reproductive activities by other members of the species; (4) provision of an adequate food supply for rearing the young; (5) reduction of loss to predators; (6) reduction of time spent in aggression; and (7) prevention of epidemics.

The controversy concerning the biological functions of the territory stems mainly from the lack of quantitative empirical data. This deficiency was basically why Hinde (1956) concluded that little progress had been made in assessing the functions of the territory since the book by Howard in 1920.

Perhaps the most controversial of the presumed functions is that of ensuring a food supply for the parents and offspring. This matter can be examined only in those situations in which all needs are met within the confines of the area defended (Type A territory of Nice, 1941, and Hinde, 1956). Critics of this presumed function have pointed to the wide differences in sizes of breeding territories within one species as circumstantial evidence negating this proposition (Lack, 1954, p. 260). For example, Kendeigh (1941b) found that the largest territories of the house wren (Troglodytes aedon) were 10 times the area of the smallest, and Lack (1948) reported a five-fold difference in the European Robin (Erithacus rubecula). However, Stenger (1958) demonstrated close correlations between size of territory in the ovenbird (Seiurus aurocapillus) and food production in each of several habitats in Ontario, thus provid-support for the food-supply hypothesis.

Further confusing this issue was the discovery of Beer et al. (1956) that the spatial requirements of several species of song birds nesting on small islands in Basswood Lake, Minnesota, were much smaller than those of mainland populations. Territories of successfully breeding song sparrows (Melospiza melodia) were one-tenth the size of those on the mainland. Parallel results were obtained for the yellow warbler (Dendroica petechia) and for the Red-eyed Vireo (Vireo olivaceus) on these islands. Their findings suggested the possibility of determining the validity of the "food-value" hypothesis through the effective reduction of available food on territory by use of insecticides, while quantitatively comparing the effects of this induced stress upon the time budgets of the birds on the experimental and control territories. Such a food reduction would reduce the area for foraging and be comparable to reducing territory size or to placing birds on smaller islands.

Although descriptive studies focusing on territoriality as a behavioral phenomenon have been carried out, a quantitative study of information concerning the utilization of the territory, even in one species, is inadequate. This investigation proposed a comparison of the time and energy budgets of the males of nesting pairs of yellow warblers to determine the utilization of their available time and also to determine specific behavioral relationships with the habitat.

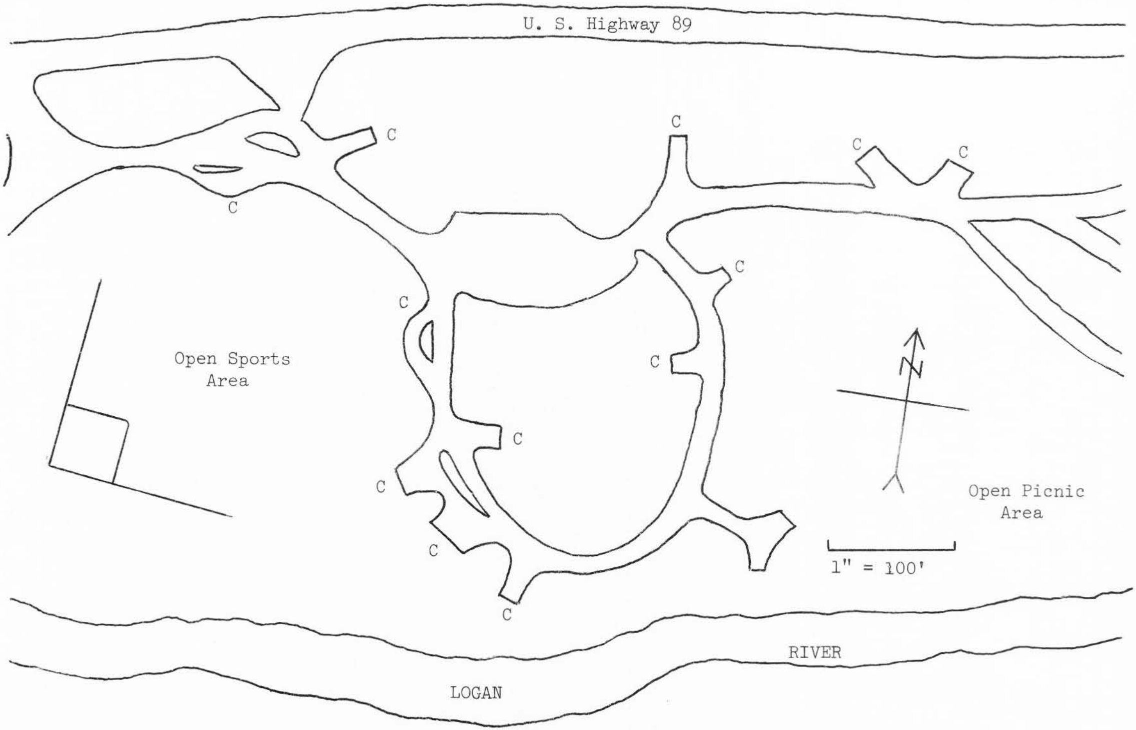
The yellow warbler was selected for this study because of its abundance, small territory size, the restriction of its foraging mainly to the gleaning of the leaf surfaces of the canopy layer of vegetation, and insectivorous food habits. Its territory fits the "Type A" category.

The Study Area

The study area was located within a U. S. Forest Service campground in the floor of Logan Canyon, 7 miles east of the post office of Logan, Utah. A network of roads traverses it, and, especially in campsite areas, some clearing of trees and underbrush had been carried out (Figure 1). The Logan River flows along the south side of the area, and the mountain slopes rise sharply on either side. This topography produces a linear habitat approximately 200 yards wide.

The vegetational cover of the valley floor is a deciduous woodland with some grassy open areas. Except in the campsites there is considerable underbrush composed mainly of wildrose (*Rosa woodsii*), hawthorn (*Crataegus rivularis*), blueberry elder (*Sambucus coerulea*), dogwood (*Cornus stolonifera*), and sierra willow (*Salix wolfii*). The dominant, canopy-forming trees of the area are box elder (*Acer negundo*), dusky willow (*Salix melanopsis*) and river birch (*Betula fontinalis*). Large trees of lesser abundance are native alder (*Alnus tenuifolia*), narrow-leaf cottonwood (*Populus angustifolia*) and green ash (*Fraxinus lanceolata*).

The north-facing slope flanking the area is covered with a mixture of Douglas fir (*Pseudotsuga menziesii*) and Utah juniper (*Juniperus osteosperma*). The south-facing slope is covered with Rocky Mountain maple


U. S. Highway 89
C
C
C
C
C
C
C
C
C
C
C
C
Open Sports Area
Open Picnic Area
1" = 100'
RIVER
LOGAN

(*Acer glabrum*) and Utah juniper. Neither of these vegetation types was occupied by yellow warblers.

Brief Life History of the Yellow Warbler

Wintering grounds

The subspecies *morcomi*, which nests in the Great Basin region, winters in Central America and western Peru (Griscom and Sprunt, 1957).

Spring arrival dates

The first arrivals were noted in the vicinity of Logan, Utah, from April 29 to May 4. However, the main concentration of males usually was not present until May 7 or 8. The latest new arrival was recorded on May 28; however, the appearance of this individual may have represented a case of local resettling.

Reproductive activities

The female selects the mate, probably basing her choice on the behavior of the male and on the nesting habitat. Nest building begins soon after the arrival of the female, approximately May 19 to as late as June 9, and requires approximately four days for completion. The male does not aid in building the nest.

Copulation takes place during the same interval as nest building. Observed dates were from May 18 to 27, inclusive. The female appears to be the initiator of copulation, following the male through the trees giving begging calls and fluttering her wings. The male remain reproductively active until the latter part of the nestling stage and renestings are accomplished if the first nest is destroyed or fails in the early stages. I saw no indications of second nestings.

The number of eggs, calculated from 12 nests, varied from three to five, with the mode being four and the average 3.9 per nest.

Egg laying started June 2 and continued through June 21 on my study area. The earliest brood observed began hatching on June 19.

The observed incubation period was approximately 12 to 13 days. Probably the female begins incubation after laying the first egg, as the eggs hatch on successive days.

The nestling stage lasts from 11 to 14 days with a mean of 12.5 days (sample of 12 broods). Both sexes feed the nestlings.

The pair bond was active from the time of pairing until the fledgling stage. During the latter stage most females would move throughout the area feeding the fledglings without regard to territory boundaries. Territory-holding males were passive toward these groups, making no attempt to chase them from the territory.

During the fledgling stage the brood is divided between the parents, if both have survived. This could be a result of differential hatching, with the male taking the older young which leave the nest first, as discussed by Sutton and Parmelee (1955) for the lapland longspur (Calcarius lapponicus). This stage was approximately 14 days long, but varied among nests, with beginning dates occurring from July 1 to 28. The fledglings became independent when the molt of the adults was partially completed. The young wandered unrestricted throughout the area, soon leaving it permanently. No cowbird (Molothrus ater) nest parasitism was noted in this investigation.

Schrantz (1943) gives a thorough review of the nesting behavior of the Eastern Yellow Warbler (D. p. aestiva), a race similar in reproductive behavior to D. p. morcomi.

Post-nuptial molt

The initiation of the annual molt varied among individuals, both male and female, beginning from July 9 to August 1. Completion of molt was less variable, occurring from August 21 to 28. Late starters exhibited an accelerated molt progress. The average molt span per individual is approximately 6 weeks, with late starters possibly completing the sequence in 1 month (Frydendall, MS).

Fall migration

From observations and playback, banded birds on the study area started migration between August 25 and 31. However, unbanded yellow warblers were seen on the area as late as September 3 in 1965. These later individuals probably were migrating from farther north, or higher elevations locally, stopping to feed in the area during the day.

METHODS

Following preliminary investigations in 1963, an attempt was made to study the activities, both social and individual, of the males of 10 breeding pairs of yellow warblers through their reproductive cycles in 1964 and 1965. During 1965, when experimental work involving the reduction of the food supply was carried out, five males were used as controls and five were utilized as experimental subjects.

Males were captured for banding soon after their arrival, usually during the first 1 to 4 days in May. Capture in mist nets was facilitated by playing a tape recording of the male yellow warbler song on a Trans-Flyweight portable tape recorder; this was amplified through a battery-operated, transistorized speaker placed in the vicinity of a Japanese mist net. To facilitate the luring of the birds, a dummy male yellow warbler was placed alongside the net. Upon capture, two combinations of three-colored celluloid split rings and the aluminum U. S. Fish and Wildlife service band were placed on the tarsi. Certain of the rectrices were painted with Testor's airplane dope in various patterns and colors to enhance individual recognition at greater distances.

After 15 to 17 males had been banded in the study area, 10 of these were selected for further study. Twice weekly, in the interval from 5:00 a.m. to 10:00 a.m., a continuous observation period of 15 minutes was spent with each male. Three stopwatches were used to determine the amount of the time spent in foraging (including both eating and searching), territorial defense (including singing, posturing and chasing), and the amount of time the bird was lost from view. During the same time period details of behavior, species of plants occupied, specific feeding location, estimated height above the ground, and feeding method utilized were recorded on a portable tape recorder, and the recording was transcribed later.

Territorial boundaries were determined from the locations of singing posts and sites of encounters, and plotted on a U. S. Forest Service map of the campground. The outer points were connected and the area of each territory determined by planimeter. Open spaces not usable by the birds were subtracted from the total area.

Each week 30 foliage samples were taken from the three most commonly used trees, box elder, river birch and dusky willow, at heights of 6, 12, and 24 feet to provide an estimate of the insects available. These samples were taken 1 hour after sunrise, calculated from the world almanac, since the study area was situated in a valley and the sun did not strike the ground there until approximately ½ hour after the determined sunrise. The second ½ hour permitted insects to perform movements from nocturnal refuges to their customary feeding stratum of the vegetation. Collections were made by placing an 18 x 36 inch plastic bag over approximately 2 feet of a terminal branch and then severing the branch. A cotton ball saturated with chloroform was placed in the bag and the top secured with a cord. This method of collecting the insect samples was a modification of that described by Gibb and Betts (1958) and Gibb (1960).

These bags were taken into the laboratory where the insects were removed from the leaves and limbs. The contents of the bag were dumped into a large metal cylinder 2½ feet tall and 18 inches in diameter, and the branch was then struck on the side of the cylinder to knock off any dead insects stuck to the leaves. Each limb was then searched carefully for remaining insects, especially web-spinning and leaf-rolling Lepidoptera larvae. The insects were stored in vials of 70 per cent alcohol. The limbs were then placed in large paper bags and dried at room temperature (approximately 72 F) for 5 weeks and weighed to obtain the air-dried vegetation weights.

Later the insects were classified to family and air dried until the surface moisture evaporated. Then the representatives of each family were weighed on a Right-A-Weigh analytical balance to the nearest 0.1 milligram. Weights of these insects were calculated in grams of insects per 1000 grams of air-dried vegetation to reduce the error in the variability of the limb samples.

To obtain an estimate of the amount of foliage surface, on the assumption that the total surface of the foliage of a given tree was proportional to the cross-sectional area of the trunk, the diameter at breast height was taken for each representative of the three basic canopy-forming trees (box elder, river birch and willow). The total diameter at breast height was then multiplied by the grams of insects per 1000 grams of dry vegetation weight of each of the three species to obtain a comparative food-value index for each territory.

Each week six yellow warblers were collected from similar habitats adjacent to the study area for the determination of the foods being taken by these birds. To minimize crippling loss and to reduce collection time, the warblers were drawn in to close range by playing back the tape recording of the male yellow warbler song. They were then collected, using a .22 caliber rifle and bird-shot cartridges. In order to prevent the rapid autolysis of food particles by gastric juices, as described by von Koersveld (1950), 1 ml of 10 per cent formalin was orally injected into the digestive tract. The birds were then taken to the laboratory where the esophagus, proventriculus and ventriculus were removed and the contents washed into a vial of 70 per cent alcohol. Later the contents were determined to arthropod order, and the numbers of specimens in each order recorded.

On June 7, 1965, approximately 20 per cent of the area of each of five experimental territories was sprayed to reduce the insect population. The spray selected was a synthetic carbamate, Sevin[1] (2-Naphthyl-N-methylcarbamate), which is of low toxicity to vertebrates and has a short residual effect (approximately 30 days maximum, depending upon climatic conditions) (CRAG Agricultural Chemicals, 1961). Spray was applied with a "John Beam" orchard sprayer at 250 pounds of pressure with the efficiency of spraying approximately 40 to 50 feet in height. The concentration of insecticide used was 1½ pounds of 50 per cent wettable Sevin per 100 gallons of water. Approximately 1000 gallons were applied per acre. Insect weights from the sprayed and unsprayed trees were compared weekly to determine the percentage of the insect population destroyed.

Because of the slight differences in intervals between calendar dates of data collection between and within years the specific dates of collection are given in Table 1. Throughout the dissertation the data will be given according to the weeks listed in the column on the left.

Data were handled statistically by using the group comparison Student's-t test, analysis of variance, orthogonal comparison, Duncan's multiple range test, and chi square, according to methods presented by

---

[1]Registered trademark of Union Carbide Corporation.

Snedecor (1956); in all cases significance was at the 5 per cent level to determine significant differences.

Nomenclature of the vegetation followed that of Holmgren (1965), that for insects and other arthropods, Borror and DeLong (1964).

Table 1. Specific dates of data collection for the years 1964 and 1965

Week	Month	Activities[a]		Foliage samples		Specimen collection	
		1964	1965	1964	1965	1964	1965
1	June	9-11	8-12	10	9	12	11
2		17-19	15-19	18	17	20	18
3		23-25	21-23	24	22	26	25
4		29- 1[b]	29- 1[b]	30	30	2	2
5	July	7- 9	6- 8	8	7	10	9
6		14-16	13-15	15	14	16	16
7		20-22	20-22	21	21	23	23
8		29-31	27-29	30	28	31	30
9	August	4- 6	3- 5	5	4	7	7
10		11-13	10-12	12	11	14	13-14
11		19-21	17-19	20	18	21	21
12		25-27	24-26	26	25	27	27-28

[a]The activities included foraging, territorial defense, and resting and preening.

[b]July date fell in week's activities.

RESULTS

Food Availability and Utilization

Insect availability

The seasonal pattern of availability of insects is shown in Figure 2. Considerable variability is evident in this graph, especially in the data for 1964 and the unsprayed areas in 1965. This variability probably is due to two main factors. The first is the small numbers of insects actually obtained, a result of the relatively small vegetation samples. The distribution of Lepidoptera larvae provides another possible explanation for the erratic fluctuations. Many larvae of this order tend to be gregarious and, after hatching, they usually remain in close proximity to their natal area because of slow dispersal. Accordingly, limb samples may not have provided an unbiased sample, and a larger number of samples would have been needed to remove this sampling error.

The effect of the spraying on the insect populations is indicated in Figure 2. By group comparison test significantly fewer insects were present on the sprayed area from June 9 through July 28, 1965, with the exceptions of June 22 and July 14. Sampling error may explain the lower insect weights on the control area on the latter two dates. Effects of the spray seemingly wore off by the first part of August, 1965, and the insect distribution in the sprayed and unsprayed areas coincided thereafter (Figure 2).

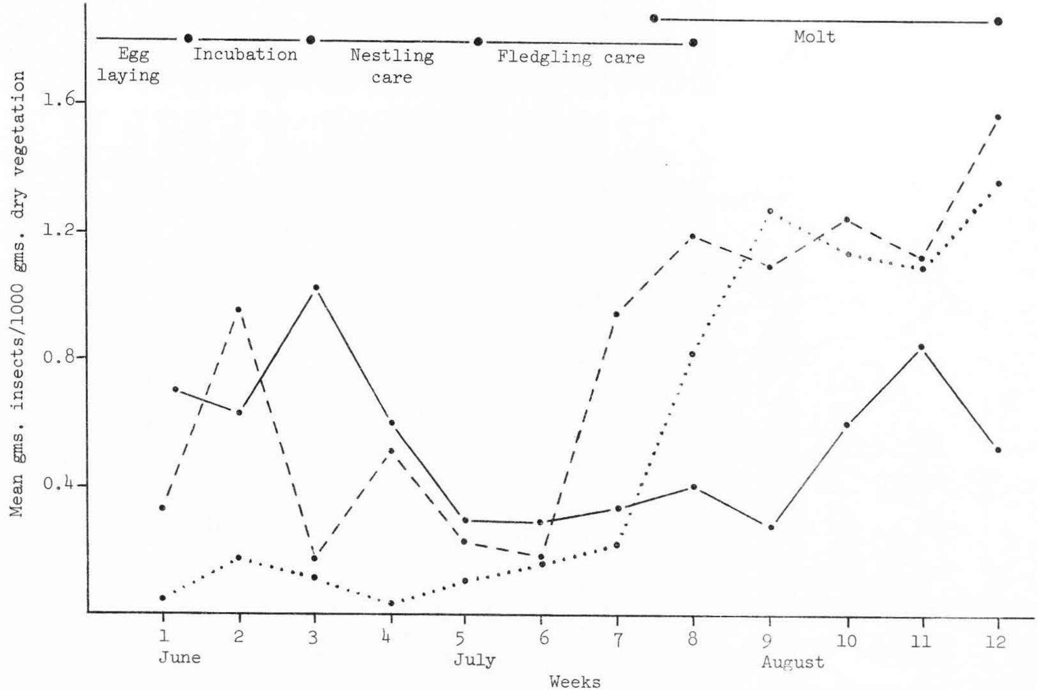


Figure 2. Average weights of insects per 1000 grams of dry vegetation available for 1964 (solid line); unsprayed areas, 1965 (broken line); and sprayed areas, 1965 (dotted line).

Throughout the investigation periods in 1964 and 1965 there was no significant difference (analysis of variance, ANOV) in the insect volumes from foliage samples taken at 6, 12, and 24 feet. However, in both years there was a significant difference (ANOV) in the amounts of insects available per species of tree. In both years the population levels of arthropods per weight-unit of foliage in river birch and box elder were similar, whereas dusky willow had smaller quantities of available insects (Table 2 and Figures 3 and 4). The fluctuations at the latter part of the summer of 1965 (Figure 4) probably resulted from the sampling method. The peaks in box elder on July 21 and 28, 1965, are attributable to Lepidoptera larvae, but on August 25, 1965, large numbers of Forficulidae (earwigs) were responsible for the peak. Also, the disproportionate weights in the dusky willow for August 4, 11, and 18, 1965, were due to Lepidoptera larvae and to earwigs.

Table 2. Biomass of arthropods in foliage of the three principal tree species, expressed as average mg. of insects per 1000 grams dry foliage

	Mg. of arthropods		
	Box elder	River birch	Willow
1964	0.6670	0.7586	0.2114
1965 (unsprayed)	0.5102	0.8639	0.3640

This differential in insect availability among the three species of trees also is reflected in the number of different insect families found on their foliage. Box elder and river birch supported the greatest

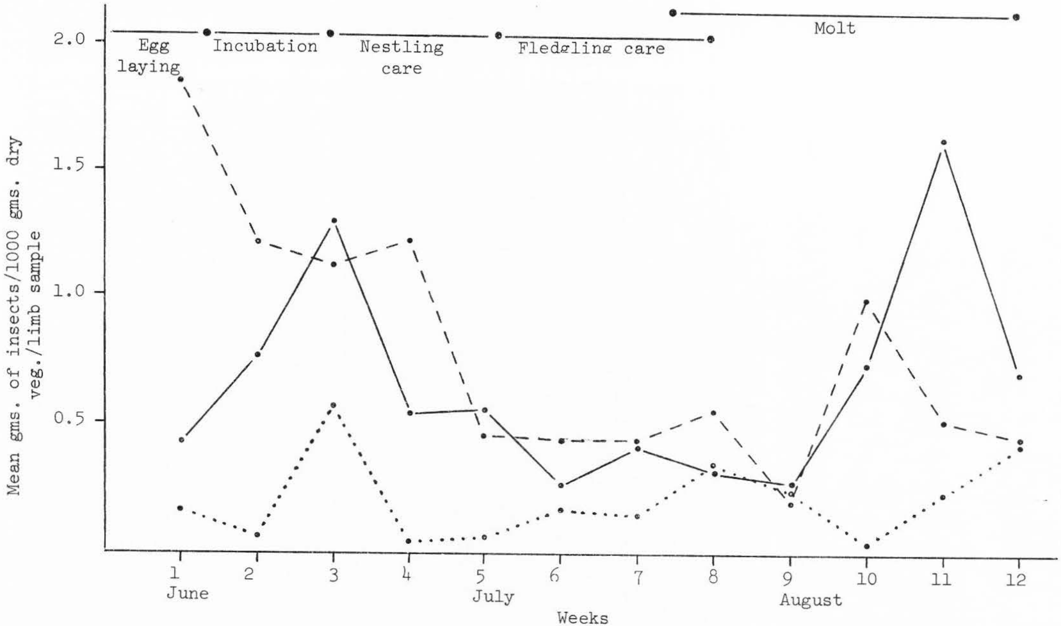


Figure 3. Weights of insects present on the foliage samples from box elder (solid line), river birch (broken line), and dusky willow (dotted line) for 1964.

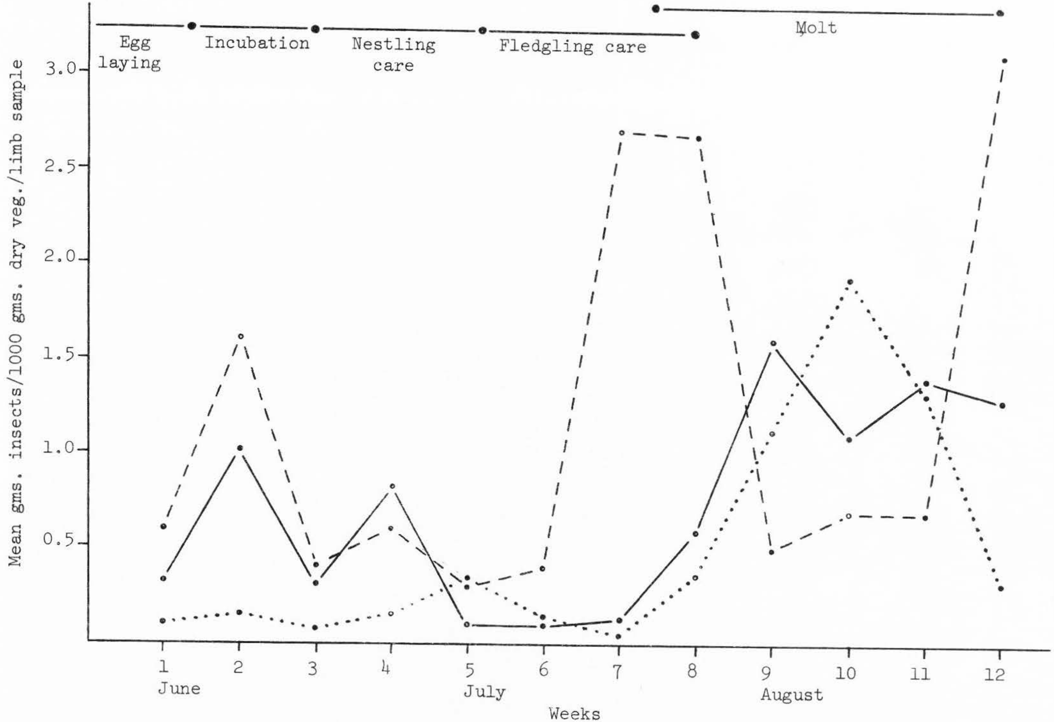


Figure 4. Weights of insects present on the foliage samples from box elder (solid line), river birch (broken line), and dusky willow (dotted line) for the unsprayed areas in 1965.

number of families in both years, with dusky willow supporting few (Table 3).

Table 3. Number of insect families represented in foliage samples of the three most commonly utilized trees in 1964 and 1965 (unsprayed)

Weeks	Box elder 1964	Box elder 1965	River birch 1964	River birch 1965	Willow 1964	Willow 1965
1	10	6	9	7	6	6
2	10	8	9	6	6	5
3	11	9	10	7	9	5
4	8	10	10	7	7	4
5	10	8	13	6	7	5
6	11	9	17	9	6	3
7	10	8	13	10	11	2
8	11	13	10	6	9	6
9	8	18	8	8	4	6
10	12	13	11	9	5	7
11	9	9	8	6	4	7
12	8	7	7	9	8	5
Average	9.8	9.8	10.4	7.5	6.8	5.9

Stomach contents

An analysis of the stomach contents of yellow warblers was undertaken to determine the foods being taken in relation to those available, and to determine if the yellow warblers were eating other types of food not detected during observation. Due to autolysis of food particles and grinding by the ventriculus, before collection of the birds, the specimens in the stomach were identified only to order.

In most cases, except for Acarina and Orthoptera, orders found on the foliage were also found in the stomach contents (Table 4). The absence of Acarina in the stomachs was possibly due to their small size. Either the birds did not feed on them or they were digested so rapidly that none was recorded.

Table 4. Occurrence of arthropods of various taxa in foliage samples and in "stomach" contents expressed as percentage of number of individuals

Order	1964		1965	
	Foliage	Stomach	Foliage	Stomach
Hemiptera	31.0	12.5	9.9	16.3
Acarina[a]	14.6	--	5.4	--
Homoptera	23.2	9.5	51.6	10.2
Araneida[a]	9.0	1.9	10.4	1.9
Lepidoptera	8.6	7.9	8.0	4.4
Coleoptera	5.2	15.8	3.9	7.6
Hymenoptera	2.4	32.3	3.8	23.0
Dermaptera	2.3	0.3	2.0	0.4
Diptera	1.9	18.1	3.2	31.2
Orthoptera	1.4	--	--	--
Neuroptera	0.3	0.3	0.8	0.9
Psocoptera	0.07	0.08	0.5	1.8
Plecoptera	0.07	--	0.1	1.2
Mallophaga	--	0.1	--	--
Thysanura	--	0.08	--	--
Ephemeroptera	--	0.5	--	0.9
Thysanoptera	--	--	0.4	0.07
Trichoptera	--	--	--	0.07
Odonata	--	--	--	0.2

[a]Arthropod orders other than Insecta.

The stomach contents also revealed small percentages of Mallophaga, Thysanura, Ephemeroptera, Trichoptera and Odonata, none of which was found in any foliage samples. These orders, most of which are aquatic, probably were so infrequent on the limbs that none was found.

Although Hymenoptera and Diptera were infrequently found in the samples of vegetation, they were utilized quite heavily by the warblers (Table 4). Probably this disparity was a consequence of the sampling method and not a result of differential feeding pressure. When the bags were placed over the limb, individuals of these two orders flew away, resulting in low numbers in the limb samples.

During 1964, 31 per cent of the arthropods on the limb samples were Hemiptera, but only 12.5 per cent of the stomach contents were of the same order. This would imply that the birds did not feed on insects of this order heavily, but in 1965 these data were reversed (9.9 per cent on the limbs and 16.3 per cent in the stomach contents). A possible reason for this difference could be that in 1964, 64.4 per cent of the Hemiptera were of the family Lygidae, whereas in 1965 no lygids were found. The lygids contain scent glands and release a pungent odor; apparently these insects were not utilized as food by the yellow warblers.

Homoptera also appear to be lightly utilized as food, but a large number of the Homoptera found on the limbs belonged to the family Aphidae, characterized by soft bodies. Probably these were digested so rapidly that relatively few of them could be identified in the stomach contents.

Coleoptera appeared to be preferred, with adults making up nearly all of the individuals of this order utilized and larvae being fed on only infrequently.

Insects of five orders, Hemiptera, Homoptera, Coleoptera, Hymenoptera, and Diptera, make up most of the diet of the yellow warbler. In 1964 and 1965 these five orders made up 88.2 and 88.3 per cent of the diet by weight, respectively.

Food-value index

The comparative food-value index for each territory shows that there was considerable variation among territories. In most cases the larger territories had the greatest food-value index, but the ratio was not always directly proportional (Table 5). Probably this deviation was a result of disproportionate coverage of canopy-forming trees. Some territories had larger areas of low shrubs without canopy covering them. These were not calculated in the food-value index but were utilized by yellow warblers, especially when feeding fledglings. The low shrubs without canopy were utilized less than 5 per cent of the time for the most part.

During 1964 the food-value index for the largest territory was five times greater than that of the smallest, and in 1965 the largest was seven times greater before spraying in early June. Food value was proportional to size, with a significant correlation of 0.9 (Figure 5).

Territory

Territory establishment

Establishment of the territory takes place immediately upon the arrival of the male yellow warblers. The first males arrive during the first few days of May, and in most cases territories are well established before the arrival of the females approximately 1 week later.

Table 5. Food-value index in relation to the territory size, estimated from the three principal canopy-forming trees

	1965					1964		
		Food-value index[a]			Food-value index			
		May 26	June 15					
Territory	Size in acres	Entire territory	Unsprayed portion	Size in acres	August 26 Entire territory	Territory	Size in acres	Food-value index
Control								
1	.21	11.5	11.5	.21	11.5	A	.13	10.1
2	.27	22.2	22.2	.27	22.2			
3	.35	31.4	31.4	.28	26.2	B	.27	19.8
4	.71	65.4	65.4	.65	54.2			
5	.63	35.3	35.3	.43	34.7	C	.48	27.1
Mean	.43	33.2	33.2	.37	29.8	D	.29	13.0
						E	.22	10.2
Experimental								
6	.23	14.0	10.5	.23	14.0	F	.39	47.3
7	.33	21.2	17.4	.43	32.7			
8	.32	26.8	--	--	--	G	.22	23.5
9	.31	20.4	15.5	.29	18.9			
10	.17	9.3	7.6	.33	18.4			
Mean	.27	18.5	12.8	.32	21.0			
Combined mean	.35	25.9	24.1	.35	25.9		.28	21.5

[a]Food-value index is the seasonal average grams of insects/1000 grams dry vegetation times diameter of tree at breast height.

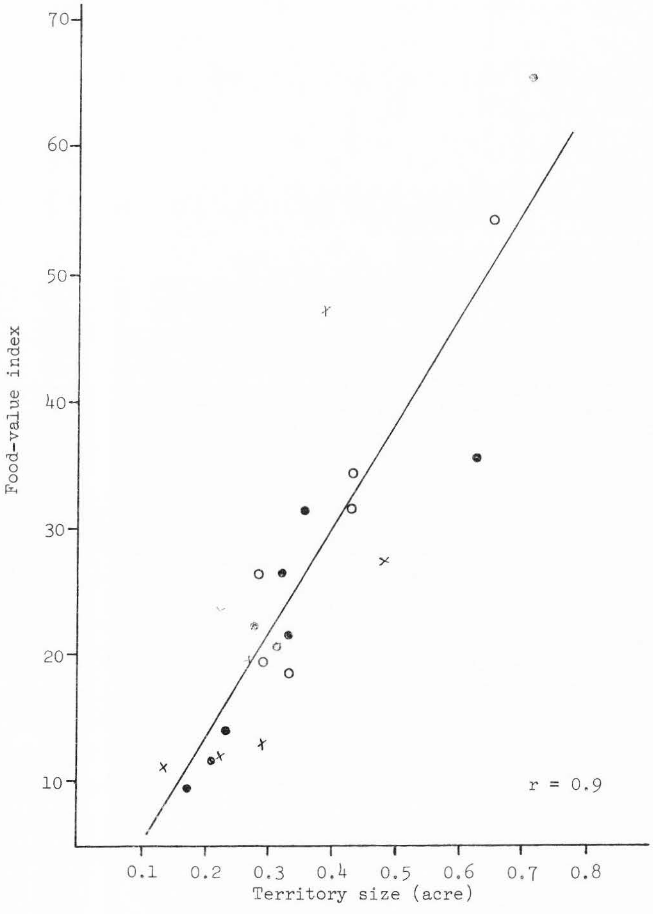


Figure 5. Relationship of territory size to food value. ●, May 26, 1965; o, August 26, 1965; and x, August 27, 1964.

During 1964 the yellow warblers were first observed on May 2, at Logan; however, none was observed at the study area until May 8. After this time they moved in rapidly and the area was filled by May 12; territory boundaries were fairly well defined by that date.

The first arrival date for 1965 was May 1, and a dense population was present by May 3. However, on May 5 and 6, there was inclement weather with rain, snow, heavy winds, and temperatures around 25 F at night. During these 2 days all yellow warblers disappeared from the area. Conceivably, this was a case of reverse migration as described by Lewis (1939). Possibly these birds moved southward to areas of more moderate temperature and waited until the weather cleared. The yellow warblers did not reappear on the study area until May 10, and the population was not well established until May 17. Boundary conflicts were still prevalent through May 22.

Territory size

First arrivals tend to occupy large areas through which they forage and sing, with few clashes with their neighbors. However, as the population density increases, the area occupied by each individual is reduced accordingly. Such a reduction was found by Mickey (1943) while studying a population of McCown's Longspur (Rhynchophanes mccownii) in Wyoming. Figure 6 shows a similar reduction in the territory of an early arrival (banded May 10, 1965, double solid line) which claimed an area of .95 acre. However, as other individuals arrived and the density increased, his territory was reduced bit by bit. On May 14 he lost two sections to two new arrivals (1 and 2), and on May 15 lost two additional portions (3 and 4). On May 17 a banded bird (5) which had held the same area the year before pushed him completely out of the area, and he was not seen

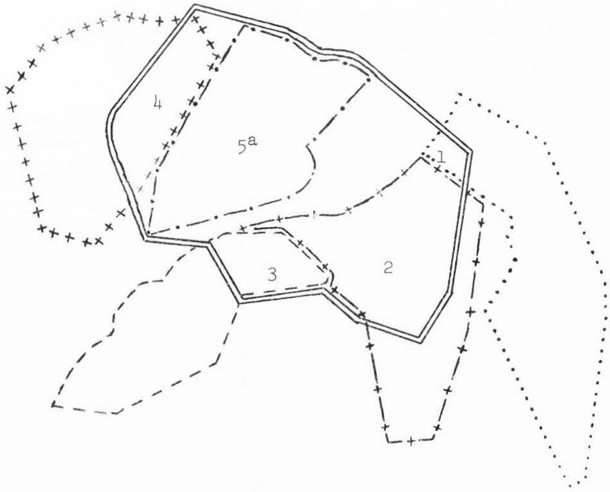


Figure 6. Map showing progressive partitioning of an early-established territory. Double line represents the territory of the first arrival; other boundaries represent later arrivals which claimed portions of the large territory and remained. See text for further explanation. [a]Banded returnee.

again. Presumably then, territory size would be much greater in areas of low density, being compressed as density increases.

During 1964 the seven territories investigated averaged .29 acre, ranging from .13 acre to .38 acre (Table 6). Territories of similar size were recorded for the yellow warbler by Beer et al. (1956) and Kendeigh (1941a). Although Figure 7 suggests a low density, those individuals under investigation were scattered throughout the study area, and all the suitable intervening space was utilized by other, unbanded birds. In all cases there were abutting boundaries, except where boundaries bordered open areas. A similar situation existed in 1965.

The sizes and distribution of the 10 territories with which the experimental portion of the investigation was conducted in 1965 are shown in Figure 8. Just previous to the spraying, the territories varied from .63 to .17 acre, with a mean of .35 acre. After the time of spraying (June 7, 1965) the territories of the control birds (those from unsprayed areas) showed no noticeable fluctuation. However, on May 28, 1965, an unbanded bird moved into the center of territories 3, 4, and 5 and carved out a territory by taking a portion of each of the three listed territories (Table 6 and Figure 8). By May 31, 1965 the birds in territories 3, 4, and 5 had lost 20, 8.5, and 31.8 per cent of the territories, respectively (Table 5), with the unbanded bird then controlling .32 acre.

The birds from the sprayed territories adjusted their territorial boundaries noticeably (Figure 8). However, it appeared that much of this activity was due to circumstances other than the food reduction.

The male from territory 10 (sprayed) increased his territory 94.1 per cent from the second week in June, holding this larger area thereafter. The female of this pair selected a nest site completely off the

Table 6. Sizes of territories and numbers of trespasses in 1964 and 1965 and comparisons of the experimental and control territories in 1965

	1965						1964		
	Territory size in acres May 26	Territory size in acres Aug. 26	Percentage of area sprayed June 7, 1965	% increase	% decrease	No. trespasses observed		Territory size in acres	No. trespasses observed
Unsprayed									
1	.21	.21	--	--	--	--	A	.13	2
2	.27	.27	--	--	--	1	B	.27	-
3	.35	.28	--	--	20.0[a]	--	C	.48	-
4	.71	.65	--	--	8.5[a] [b]	2	D	.29	1
5	.63	.43	--	--	31.8[a]	--	E	.22	3
							F	.39	-
Sprayed							G	.22	-
6	.23	.23	26.1	--	--	15			
7	.33	.43	24.2	30.3	--	--			
8[c]	.32	--	18.8	--	--	1			
9	.31	.29	22.6	--	6.5	--			
10	.17	.33	23.5	94.1	--	--			
Average	.35	.32	--	--	--	--		.29	-

[a]May 28, 1965. Before spraying. Appropriated by newcomer which acquired .32 acre.

[b]Unbanded bird which took this percentage had a territory .32 acre.

[c]Lost early in season on June 19, 1965.

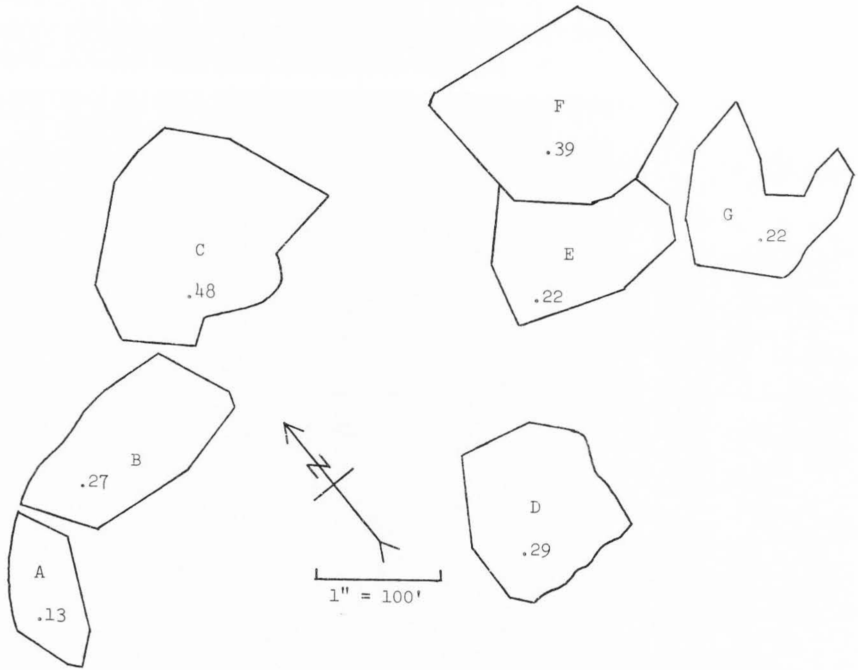
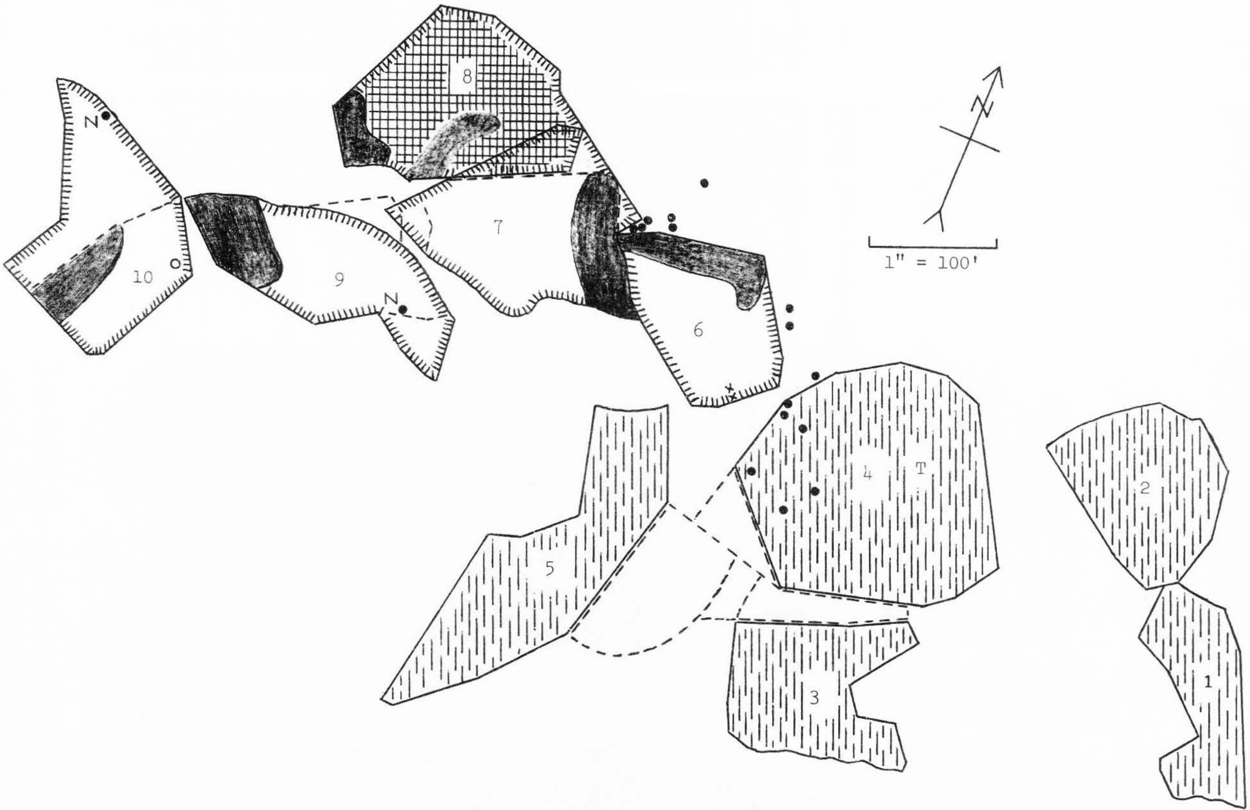


Figure 7. Disposition and size relationships of the territories for 1964. Values indicate acreage of the territory.



N
1" = 100'
1
2
3
4
T
5
6
7
8
9
10
N
N

territory invading an unbanded yellow warbler's territory; probably the reason for the increase was to include the nest site (Figure 8).

A portion of male 9's territory (sprayed) was taken by male 7. Territory 9 was extended to the southeast, but still decreased 6.5 per cent to an area of .29 acre. The female selected a nest site exactly on the territory boundary, and again the increase in area was probably a result of the female's activity.

The male from territory 8 was of very little value to the study, since he disappeared 1½ weeks after spraying. Since his territory was situated on both sides of the highway, he may have been killed by a passing vehicle.

The territory of male 7, a banded returnee from 1964, showed considerable change. Soon after the disappearance of the male from territory 8, male 7 increased his territory 30.3 per cent. A probable explanation for this increase is that he absorbed a portion of the territory held by male 8 after the latter's disappearance (Figure 8 and Table 6).

The remaining experimental territory (number 6) showed no size change throughout the season. However, this individual did not honor the territory boundaries. He trespassed an observed total of 15 times in 4.3 hours that he was under surveillance, whereas only four other trespasses by the remaining nine birds were noted (Table 6). However, 12 of the 15 trespasses took place during the latter part of the fledgling stage, and probably the male followed the young he was feeding into the surrounding territories. In three of these instances the holder of the territory into which he and the fledgling trespassed was present but showed no aggressive action.

Response to playback

Observations of the responses of male individuals to a dummy yellow warbler in 1964 suggested a tendency toward increased aggressiveness during the incubation stage. In 1965, to obtain an indication of this change, records were kept of the percentage of males attacking the dummy during playback experiments (Table 7).

There appears to be an abrupt change in response during incubation (Table 7). Unfortunately, no data were collected in the interval from May 28 to June 11, 1965, the period when this change came about. Possible a gradual increase would have been noted during this interval.

This assumption was supported by other data. The percentage of time which the birds spent defending their territories increased from the second week in June to the second week in July. The method of territory defense changed concurrently. Chasing became more evident in the third week of June, continued until mid-July, and then decreased (Table 16). In 1964 and 1965, respectively, 80 and 75 per cent of the chases were recorded from June 15 to July 15.

This tendency toward increased aggression could have been a result of one of several factors or possibly a combination of these factors. First, it could possibly indicate that the territory is important for isolation of the pair during nesting activities, since the increase in aggression does come at the time when the female is incubating or perhaps earlier (Table 7). Disruption of the cycle by intruding males at the time of incubation would possibly affect nesting success (Armstrong, 1965, p. 281). Presumably there has been an evolutionary trend toward survival of offspring of those males who defend their territories more tenaciously at

Table 7. Response of male yellow warblers to playback and dummy during 1965

Date	No. of males subjected to playback	No. of males which attacked dummy	Stage of cycle
May 11	1	0	
May 12	2	1	
May 14	2	0	
May 17	3	1	
May 19	5	0	Pair formation and copulation
May 21	7	2	
May 22	6	2	
May 28	3	1	Nest building and egg laying
June 11	7	6	
June 18	7	6	Incubation
June 25	8	6	
July 2	8	6	
July 9	7	5	Nestling care
- - - Regression of testes[a] - - -			
July 16	10	1	Fledgling care
July 23	9	1	
July 30	14	1	
Aug. 7	12	0	Molt
Aug. 13-14	17	0	
Aug. 21	12	0	
Aug. 27-28	14	0	

[a] Regression of the testes was determined when the mean diameter of the testes was 50 per cent the size of those of the early breeding season. This was determined from 139 specimens.

this time. Observance of an increase in the vigor of territorial defense at this time lends support to this idea.

Second, this increase in aggressiveness could be a result of increased confidence of the males after having won numerous encounters earlier in the season.

I believe that neighbor recognition (Weeden and Falls, 1959) can be ruled out as a factor involved in increased aggressiveness at this stage of the breeding cycle. If it were a factor, territorial defense would be expected to decrease after territories were firmly established. The opposite was observed (Table 7). These speculations are sketchy and need considerably more investigation to determine which factor, or factors, is or are more important.

Site attachment

Returning to a specific site in the habitat each spring appears to be quite common in the yellow warbler. Of 17 males which returned to the area, 10 held territories almost precisely the same as their previous ones (Table 8). Of the remaining seven males, five returned to nearly the same location and only two moved a considerable distance. Lack (1954. p. 261) suggested that the habit of breeding in the same site in successive years is probably advantageous, as birds are likely to be more successful in places with which they are familiar. In yellow warblers, familiarity with the specific area seemed to increase the aggressiveness of the returning males, aiding them in expelling unmarked intruders, presumably newcomers already settled there (Figure 6). The revival of territorial defense just before migration appears to be a means by which the males strengthen their territorial bonds (Figure 10), and it may facilitate their re-establishment should they survive until the next spring.

Table 8. Site specificity of the returning banded yellow warblers

	Present during 2 years	Skipped second year, returned in third	Present during 3 years
Reoccupied nearly identical territory	6	1	3
Returned to near vicinity[a]	4	0	1[b]
Returned a considerable distance from first year's site	1	1	0

[a]The second year's territory usually included a minimum of 60 per cent of the previous year's territory.

[b]In the second year he moved a considerable distance from the previous year's territory, but in the third year his territory was almost exactly the same as the second year's.

Time Budgets

A survey of the time budgets of males was undertaken to determine what proportion of time was occupied in feeding, territorial defense, and resting and preening during the breeding season. At the same time, data on vertical level of activity, types of activity, and species of tree or shrub occupied were collected.

During the experimental phase of 1965, orthogonal comparisons demonstrated that the males from the sprayed and unsprayed territories differed significantly in the height and method of foraging and defending the territory, and in the frequency with which they utilized different species of trees in foraging. However, it is believed this was a result of the variability of individuals between and within groups, because of the small sample size, and that no biological significance exists. Therefore, data for birds from the sprayed and unsprayed territories have been consolidated in the results involving the above-mentioned activities. Tables reporting these activities, separated into sprayed and unsprayed territories, are given in Appendixes A and B.

Feeding activities

Feeding method.--Only three methods of feeding by the yellow warbler were noted. These were gleaning while perched (basically on the leaves and supporting twigs and quite infrequently on the bole of the tree), hawking (flying into the open and catching a flying insect), and hovering (fluttering in a stationary position and picking an insect off a leaf).

Gleaning on leaves was used most often (Table 9 and 10). Searching and gleaning on the tree bole made up only 0.7 and 1.2 per cent of the observations for 1964 and 1965, respectively. In all instances except two, utilization of the bole occurred on river birch (Tables 9 and 10). In every case of utilization of the bole of the river birch the warblers were feeding at holes drilled by yellow-bellied sapsuckers (*Sphyrapicus varius*). It could not be determined whether the yellow warblers were feeding on insects attracted to the tree sap or were utilizing the sap itself. Only one individual was observed using the bole of box elder. and this was searching for insects on a dead and rotted portion (Table 9).

Hovering and hawking are utilized in nearly the same proportions, a total of 2.7 and 2.2 per cent in 1964 and 2.8 and 1.4 per cent in 1965, respectively (Tables 9 and 10). The largest percentage of the hawking and hovering is associated with box elder, river birch, and dusky willow (Tables 9 and 10). There are probably two reasons for this. First, these three species are occupied more frequently during all foraging; second, during the molt, when the birds are least able to perform these airborne movements, they forage in the lower underbrush.

Table 9. Feeding method associated with all species of plants utilized in 1964, expressed as per cent of observations. Gl T L, gleaning on terminal leaves; Gl B, gleaning on bole

Species of tree	Feeding method	Weeks (June) 1	2	3	4	(July) 5	6	7	8	Average
Alder	Gl T L	--	100	--	100	100	100	--	--	100
Green ash	Hawk	--	--	25	--	--	--	--	--	20.0
	Gl T L	--	--	75	--	100	--	--	--	80.0
Dogwood	Hawk	--	20	--	--	--	--	--	--	6.7
	Gl T L	--	80	100	100	--	--	--	100	93.3
Wild rose	Gl T L	--	--	--	--	100	--	--	100	100
River birch	Hover	--	--	3.6	--	7.2	7.7	7.7	--	4.1
	Gl B	--	33.3	--	--	7.1	--	--	--	2.0
	Gl T L	100	66.7	96.4	100	85.7	92.3	92.3	100	93.9
Willow	Hover	--	--	--	7.1	3.3	--	--	3.8	2.4
	Hawk	--	--	--	3.6	--	5.6	--	--	1.2
	Gl T L	100	100	100	89.3	96.7	94.4	100	96.2	96.4
Box elder	Hover	--	--	--	3.9	3.1	5.9	1.1	5.0	2.5
	Hawk	8.3	--	3.8	5.9	4.7	2.3	1.0	--	2.8
	Gl B	--	4.1	--	--	--	--	--	5.0	0.7
	Gl T L	91.7	95.9	96.2	90.2	92.2	91.8	97.9	90.0	94.0
Averages	Hover	--	--	0.8	3.9	3.5	5.0	1.5	3.2	2.7
	Hawk	5.0	4.4	2.4	3.9	2.6	2.4	0.8	--	2.2
	Gl B	--	4.3	--	--	0.9	--	--	1.6	0.7
	Gl T L	95.0	91.3	96.8	92.2	93.0	92.6	97.7	95.2	94.4
Number of observations		76	73	123	103	114	121	131	63	804

Table 10. Feeding method associated with all species of plants utilized in 1965, expressed as per cent of observations. Abbreviations as in Table 9

Species of tree	Feeding method	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Wild rose	Gl T L	--	--	--	--	--	--	--	--	--	--	100	100	100
Hawthorn	Gl T L	--	--	--	--	--	--	100	--	--	--	--	--	100
Dogwood	Hover	--	--	--	--	--	--	20.0	--	--	--	--	--	13.3
	Gl T L	--	--	100	--	--	--	80.0	100	--	100	100	100	86.7
Green ash	Gl T L	100	--	100	--	--	--	--	--	--	--	--	--	100
River birch	Hover	--	11.1	9.7	5.0	--	--	4.6	--	--	--	--	--	3.9
	Hawk	4.3	8.3	--	--	--	3.0	4.6	--	--	--	--	--	2.7
	Gl B	17.4	8.3	--	10.0	11.1	9.1	4.6	10.0	--	--	--	--	6.9
	Gl T L	78.3	72.3	90.3	85.0	88.9	87.9	86.2	90.0	100	--	100	100	86.5
Willow	Hover	2.1	--	2.0	6.7	3.7	3.6	--	--	--	--	--	--	2.0
	Hawk	2.3	10.5	2.0	--	--	3.6	2.1	--	--	--	--	--	2.3
	Gl T L	93.6	89.5	96.0	93.3	96.3	92.8	97.9	100	--	100	100	100	95.7
Box elder	Hover	0.8	--	1.0	4.8	4.0	6.8	3.4	4.8	--	--	--	--	2.7
	Hawk	--	1.2	1.0	--	--	2.0	--	--	--	--	--	4.8	0.7
	Gl T L	99.2	98.8	98.0	95.2	96.0	91.2	96.6	95.2	100	100	100	95.2	96.6
Averages	Hover	1.0	2.9	2.7	5.2	3.2	4.9	3.6	1.9	--	--	--	--	2.8
	Hawk	1.6	4.3	1.1	--	--	2.5	1.5	--	--	--	--	3.2	1.4
	Gl B	2.1	2.2	--	1.1	2.0	1.8	1.0	1.9	--	--	--	--	1.2
	Gl T L	95.3	90.6	96.2	93.7	94.8	90.8	93.9	96.2	100	100	100	96.8	94.6
Number of observations		192	138	183	174	155	163	195	52	41	22	74	62	1451

A comparison of food-taking methods shows that a great proportion of the feeding is carried out while perched. (Values were 95 to 96 per cent until August 3-26, when they rose to 99 per cent.) There was little difference among the first 8 weeks within the same year or between years. However, during August the amount of time spent feeding on the wing dropped considerably, because of restricted flight during the molt.

The foraging substrate.--During 1964 and 1965 food was sought on seven and eight species of trees, respectively. Of these, box elder, willow, and river birch were utilized with the greatest frequency (Table 11). The use of undershrubs (e.g. dogwood and wild rose) tended to increase in the latter part of the season (mid-July through August) mainly because fledglings are fed in this stratum. The adults tended to remain in this stratum, which affords them protective concealment through most of the ensuing molt. At this stage of the molt, soon after the fledglings have become independent, the adults have on each wing four remiges either missing or represented only by pin feathers and three to four remiges between one-half and two-thirds grown. At the same time all the rectrices have been dropped simultaneously (Frydendall, MS).

Since the three most commonly used species of trees did not occur in the same proportion, the percentage utilization is misleading. When the observed percentage utilization is compared to the proportion of box elder, willow, and river birch available, it appears that there was possibly random utilization (Table 12). Chi square tests were run on the expected and observed frequencies to test for randomness. It was found that feeding was not random in 1964. Box elder was preferred, river birch was probably fed on randomly, and willow was little used. Again in 1965, it was found that utilization was not random; river birch was highly preferred,

Table 11. Per cent utilization of each species for feeding substrate

	Weeks												
	(June)				(July)				(August)				
Species	1	2	3	4	5	6	7	8	9	10	11	12	Average
						1964							
Number of observations	73	122	103	114	121	128	63	19	--	--	--	--	743
Alder	--	--	--	1.0	3.5	4.1	5.5	--	--	--	--	--	2.3
Green ash	--	--	3.3	--	0.9	--	--	--	--	--	--	--	0.7
Dogwood	--	7.2	3.3	4.8	--	--	--	1.6	--	--	--	--	2.0
Wild rose	--	1.5	--	--	0.9	--	--	12.7	--	--	--	--	1.4
River birch	15.8	4.3	22.9	16.5	12.3	10.8	7.8	12.7	--	--	--	--	13.0
Willow	26.3	15.9	28.7	27.2	26.3	14.9	10.9	41.3	--	--	--	--	22.5
Box elder	57.9	71.1	41.8	50.5	56.1	70.2	75.8	31.7	--	--	--	--	58.1
						1965							
Number of observations	192	138	183	174	155	163	195	52	41	22	74	62	1452
Wild rose	--	--	--	--	--	--	1.5	--	--	--	4.1	2.7	0.6
Hawthorn	--	--	--	--	--	--	1.5	--	--	--	--	--	0.2
Dogwood	--	--	0.6	--	--	--	5.1	1.9	--	4.6	1.4	1.3	1.0
Green ash	1.0	--	1.1	--	--	--	--	--	--	--	--	--	0.3
River birch	12.0	26.1	16.9	11.5	17.4	20.3	22.1	19.2	63.4	--	9.4	5.3	17.8
Willow	24.5	13.8	27.3	17.2	17.4	17.1	24.6	38.5	--	13.6	27.0	34.7	21.7
Box elder	62.0	59.4	54.1	71.3	65.2	62.6	45.2	40.4	36.6	81.8	58.1	56.0	58.3

Table 12. Utilization of principal species of trees in comparison to their occurrence on the territories under study

Activity	Species	% utilization of all observations		% of individuals present	
		1964	1965	1964	1965
Foraging	Box elder	58.1	58.3	50.6	54.6
	Willow	22.5	21.7	32.7	32.2
	River birch	13.0	17.8	16.7	13.2
Territory defense	Box elder	49.6	58.9	50.6	54.6
	Willow	35.8	29.8	32.7	32.2
	River birch	12.2	10.9	16.7	13.2

box elder preferred, and willow avoided. In both years the weights of insects on willow foliage were notably lower than those on the other trees (Table 13).

Feeding height.--There appears to be no innate limitation to a specific stratum, for birds were observed foraging at levels estimated from 1 to 55 feet. The greatest height of feeding appears to be determined by the height of the vegetation; however, in no case was a male yellow warbler observed foraging on the ground. Females were observed on the ground, but in all cases were gathering nest materials.

Even though there is no restricted foraging stratum, most of the time feeding is spent in a belt 20 to 25 feet above the ground (Table 14). From my impression, the differences in the average feeding heights between 1964 and 1965 (e.g. box elder, 1964, 23.7; and 1965, 29.9 feet) may reflect differences in canopy height associated with the locations of the territories under study. Also, the disparity in mean feeding height between tree species was a result of differences in the height of the vegetation. Species of plants showing a significant difference (Duncan's multiple range test) in feeding height are given in Table 15.

Table 13. Frequency of utilization of the three most commonly used trees compared with the mean grams of insects per 1000 grams dry foliage

	1964		1965	
Species	% utilization for foraging	Mean grams insects/sample[a]	% utilization for foraging	Mean grams insects/sample
Box elder	58.1	0.6670	58.3	0.5102
Willow	22.5	0.2114	21.7	0.3640
River birch	13.0	0.7586	17.8	0.8639

[a]1000 grams dry foliage.

Observations created an impression of a decrease in the mean height of foraging during the latter part of the summer. During the fledgling period, and more prominently during the molt season, the adult birds tend to remain in the lower underbrush (see "The foraging substrate"). However, the data for mean feeding height do not support this interpretation. The probable reason for this is a lack of reproductive synchrony between pairs. Adjacent pairs may vary as much as 2 weeks in nesting chronology, and in molt the individual variation is as much as 3 to 4 weeks (Frydendall, MS). Therefore, the data for individuals that either have completed or not yet started with these cycles are consolidated, and the averages did not show individual differences.

Percentage of time spent feeding.--The percentage of time spent feeding tends to be lower in the early part of the season and increases as greater physiological demands occur. This was similar to findings of Verner (1965) for the marsh wren (*Telmatodytes palustris*), but he found a high

Table 14. Average feeding heights in each plant species on a weekly basis

	Weeks												
	(June)				(July)				(August)				
Species	1	2	3	4	5	6	7	8	9	10	11	12	Average
						1964							
Number of observations	19	73	122	103	114	121	128	63	--	--	--	--	743
Alder	--	--	--	8	19	14	16	--	--	--	--	--	15.9
Green ash	--	--	14	--	20	--	--	--	--	--	--	--	15.2
Dogwood	--	9	7	8	--	--	--	10	--	--	--	--	8.0
Wild rose	--	2	--	--	3	--	--	4	--	--	--	--	3.3
River birch	27	15	16	20	21	22	24	12	--	--	--	--	19.0
Willow	18	12	13	15	16	25	19	15	--	--	--	--	16.0
Box elder	29	19	20	24	23	24	27	22	--	--	--	--	23.7
Average[a]	25.8	16.7	16.3	19.9	20.8	23.7	25.2	15.5	--	--	--	--	20.4
						1965							
Number of observations	192	138	183	175	155	163	195	52	41	22	74	62	1452
Wild rose	--	--	--	--	--	--	3	--	--	--	4	4	3.4
Hawthorn	--	--	--	--	--	--	9	--	--	--	--	--	9.3
Dogwood	--	--	8	--	--	--	8	10	--	5	6	6	7.2
Green ash	20	--	25	--	--	--	--	--	--	--	--	--	22.5
River birch	23	24	26	27	18	21	23	24	14	--	26	33	21.9
Willow	30	19	26	19	16	18	13	10	--	13	11	18	19.4
Box elder	31	32	32	36	30	24	24	29	26	32	27	31	29.9
Average	29.6	28.2	28.9	31.0	25.1	22.5	19.8	20.3	18.5	28.4	21.6	27.4	25.8

[a]Average height of all observations.

Table 15. Statistical comparison of various activities of yellow warblers by means of Duncan's multiple range test. The numerals in horizontal rows indicate a significant difference of that species in that category of activity from the one denoted by that numeral in the left-hand column

Species	Year	Feeding height	Feeding frequency	Territorial defense frequency	Ave. ht. territorial defense
1 Box elder	1964	6-7[a]	2-3-6-7	3	3-4-6-7
	1965	6-7-8	3-6-7-8	6-7-8	6-7-8
2 River birch	1964	6-7			3-6-7
	1965	6-7-8			8
3 Green ash	1964	7			5
	1965	6-7-8			6-7-8
4 Alder	1964	7			
5 Willow	1964	7			6-7
	1965	6-7			6-7-8
6 Dogwood	1965				
7 Rose	1965				
8 Hawthorn	1965				

[a]For feeding height there was a significant difference between 1 (box elder) and 6 (dogwood) and 7 (rose). There was no significant difference between box elder and the other species of trees. This pattern of presentation is the same for all the species.

percentage of time spent foraging during the pre-nest building stage, a period when observations in this study were not made. Also Verner (1965) found that foraging time increased during the nestling stage. It would be expected that the percentage of time spent foraging would begin its increase during the nestling stage and continue to increase to a maximum point during the fledgling or molt stage and level off, but my data did not indicate this except in the sprayed territories during 1965 (Figure 9). A possible reason that no increase was evident during the nestling stage is that normally the males (the sex from which data were collected) do not feed nestlings very frequently.

There was an increase in the percentage of time spent in foraging during mid- to late-June, 1964, in spite of the abundance of insects (Figure 2). Since there was considerable rain during this month in 1964 (4.79 inches in 1964 in comparison to 2.14 inches in 1965), possibly insects remained hidden much of the time, increasing the time necessary for the birds to find sufficient food. Perhaps the birds required a greater amount of food to meet their physiological needs during the inclement weather. Another factor could be that there was a temperature drop (4 F below the annual mean) along with the inclement weather. Verner (1965) stated that insects are more active at high temperatures so they would probably be more conspicuous to a foraging bird. Thus the same number of insects might be caught in less time at high temperatures than at low temperatures with no change in the total number of insects in the environment.

The individuals from the sprayed territories spent a greater percentage of time feeding than did those of the controls in the interval after spraying (Figure 9). However, due to the great variability of

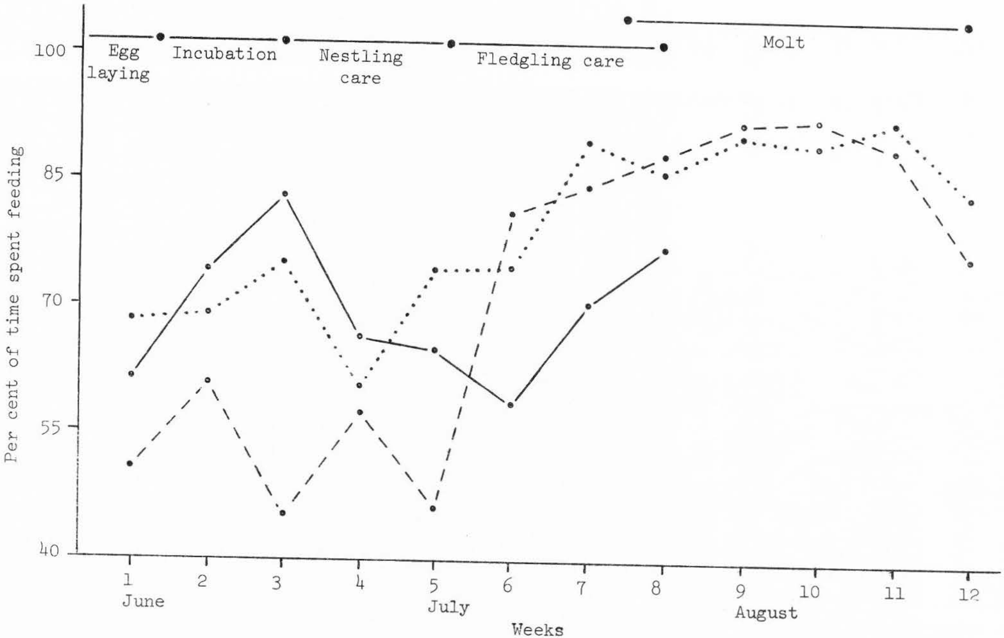


Figure 9. Proportion of the observation time spent feeding by the yellow warblers. 1964, solid line; unsprayed 1965, broken line; and sprayed 1965, dotted line.

activities during the observation periods among individuals no statistical significance could be demonstrated. This increased feeding time was probably due to the decreased amount of food, caused by spraying, and not a result of the sprayed territories being smaller, because in 1964, when no experimental spraying was conducted the birds from both the small and large territories fed about the same percentage of time, with the birds from the larger territories slightly higher. The point where percentages of feeding time came together is near the time when the insect population had rebuilt itself on the sprayed areas (compare Figures 2 and 9).

Defense of the territory

Methods of defending the territory.--The male yellow warbler defended the territory in three ways. The first of these was singing. Generally, as he foraged through the territory he occasionally stopped and sang, and then resumed foraging. It appeared, however, that there were specific singing posts where the individual perched at times for periods of 2 to 3 minutes and sang approximately once every 15 seconds. The importance of such singing posts in territorial defense in this species was noted by Kendeigh (1941a, p. 172).

The second method of defense was chasing. Whenever a male crossed the boundary into a neighboring warbler's territory, the owner flew toward the intruder. The intruder would then fly, in most cases before the owner had an opportunity to alight. The two birds would then fly in irregular circles and other figures through openings in the trees. Many times, when their territories were adjacent to an open area, they would make a large circle around it and then both would return to their respective territories. Sometimes these chases lasted 8 to 10 seconds, and an individual might fly a total distance of approximately 150 feet at one time. Only once was actual combat noted when two males locked together and fell to the ground.

A method of defense observed very seldom was posturing. When one male invaded the territory of another, the owner would fly toward the trespasser and silently alight approximately 1½ to 2 feet from him. Both birds would then assume a horizontal position, facing each other, with the neck appearing slightly stretched and the wings held out from the body and very slightly drooped and fixed. This is similar to the posturing termed "wings out" described for the chestnut-sided warbler (D. pensylvanica) by Ficken and Ficken (1962). The males would remain so perched for several seconds, until the territory owner began chasing the other as described above. Usually posturing was noted preceding the chase, but it was also noticed after a chase, before the two birds moved to their respective territories.

The type of territorial defense utilized most frequently was singing (Table 16). A comparison of the proportion of the observations that involved singing alone to that of chasing and posturing together shows that singing comprises the greatest percentage of territorial defense from early June until migration in late August (Table 16).

After banding was completed, chasing made up a total of only 2.2 and 0.8 per cent of the territory defense in 1964 and 1965, respectively. However, at first arrival in the early spring, this activity was much more prevalent, because several instances of persistent chasing when two males were vying for a common area were noted. On May 14, 1965, two birds were watched for 52 minutes, and during most of this time one bird was chasing the other through the trees (without reprisal). Finally the

Table 16. Weekly summation of methods of territorial defense performed in each plant species for 1964, expressed as per cent of observations

Species of plant	Terr. defense type	Weeks (June) 1	2	3	4	(July) 5	6	7	8	Average
Wild rose	Sing	-	-	-	-	-	-	-	100	100.0
Alder	Sing	-	-	-	-	100	-	100	-	100.0
Dogwood	Sing	-	-	-	100	-	-	-	-	100.0
Willow	Pose	-	-	-	-	4	-	-	-	0.6
	Chase	-	-	-	5	-	7	5	5	4.1
	Sing	-	100	100	95	96	93	95	95	95.3
River birch	Pose	-	33	-	-	-	-	-	-	1.9
	Chase	-	-	-	-	8	-	-	-	1.9
	Sing	100	67	100	100	92	100	100	100	96.2
Box elder	Pose	-	-	8	-	-	-	-	-	0.5
	Chase	-	8	-	-	-	2	-	-	0.9
	Sing	100	92	92	100	100	98	100	100	98.6
Total	Pose	-	5	4	-	1	-	-	-	0.7
	Chase	-	5	-	7	5	4	1	3	2.2
	Sing	100	90	96	93	94	96	99	97	97.1
No. of observations		7	19	26	56	74	102	105	36	425

pursued loser moved off to an adjoining area, where he remained for the rest of the season.

Posturing is utilized less frequently than is chasing. In 1964 only 0.7 per cent of the observations were of posturing, and no incidences of posturing were noted in 1965 (Table 17).

Utilization of vegetation.--Fewer species of woody plants were utilized for territorial defense (song perches) than for foraging. Only six and five species were employed for defense in 1964 and 1965, respectively (Table 18).

In territorial defense, as in feeding, box elder, river birch, and willow were occupied most frequently. A basic reason for this is that the males sang intermittently while feeding. Also, whenever specific singing perches were noticed they were on exposed branches in the taller trees.

During 1964 utilization of these three species was near random (chi square value of 7.49 tabular value at .05 was 5.99). Actually willow and box elder were used randomly, and a slight avoidance was indicated for river birch. The results were nearly the same in 1965, with a calculated value of 8.19 (near randomness). However, willow was utilized randomly, box elder was preferred slightly, and, again, the warblers tend to avoid river birch. This could possibly be due to the drooping nature of the river birch.

Height of defense.--Since much of the territorial defense through singing is interspersed with feeding, the vertical levels of these activities were similar. As in feeding height, there is no restricted stratum. During 1964 foraging was observed from 4 to 50 feet above ground level, and from 3 to 55 feet in 1965. The mean height of territory defense was

Table 17. Weekly summation of methods of territorial defense performed in each plant species for 1965, expressed as per cent of observations

Species of plant	Terr. defense type	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Dogwood	Sing	100	-	100	-	-	-	-	-	-	-	-	-	100.0
Green ash	Sing	100	-	100	-	-	-	-	-	-	-	-	-	100.0
River birch	Chase	-	-	-	-	-	-	17	-	100	-	-	-	1.1
	Sing	100	100	100	100	100	100	83	100	-	-	100	-	98.9
Willow	Chase	-	-	2	2	10	-	-	-	-	-	-	-	1.9
	Sing	100	100	98	98	90	100	-	100	-	-	100	100	98.1
Box elder	Sing	100	100	100	100	100	100	100	100	100	100	100	100	100.0
Total	Chase	-	-	1	1	3	-	4	-	3	-	-	-	0.8
	Sing	100	100	99	99	97	100	96	100	97	100	100	100	99.2
No. of observations		182	99	165	147	121	46	23	14	8	4	30	30	869

Table 18. The per cent utilization of each plant species for territorial defense

Species of plant	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
						1964							
No. of observations	7	19	26	56	74	102	105	36	--	--	--	--	425
Wild rose	--	--	--	--	--	--	--	13.9	--	--	--	--	1.2
Alder	--	--	--	--	1.4	--	2.9	--	--	--	--	--	1.0
Dogwood	--	--	--	1.9	--	--	--	--	--	--	--	--	0.2
Willow	--	21.0	43.2	38.9	40.0	40.2	20.9	63.9	--	--	--	--	35.8
River birch	28.6	15.8	11.5	18.5	15.7	10.8	8.6	5.6	--	--	--	--	12.2
Box elder	71.4	63.2	46.2	40.7	42.9	49.0	67.6	16.7	--	--	--	--	49.6
						1965							
No. of observations	182	99	165	147	121	46	23	14	8	4	30	30	869
Green ash	0.6	--	0.6	--	--	--	--	--	--	--	--	--	0.2
Dogwood	0.6	--	0.6	--	--	--	--	--	--	--	--	--	0.2
River birch	9.2	13.1	17.0	3.4	9.9	15.2	26.1	28.6	12.5	--	3.3	--	10.9
Willow	41.8	28.3	34.5	29.3	24.0	21.8	--	28.6	--	--	3.3	36.4	29.8
Box elder	47.8	58.6	47.3	67.3	66.1	63.0	73.9	42.8	84.5	100.0	93.3	63.3	58.9

25.2 feet and 31.6 feet above the ground in 1964 and 1965, respectively (Table 19). The difference probably reflected my selection of territories in taller stands in 1965. Some territories in 1965 had a greater percentage of taller trees.

The mean height was approximately 5 feet above that of feeding for both years (compare Tables 14 and 19). Hence, when the yellow warblers were occupied solely with singing, they tended to select higher perches, thus making themselves more conspicuous to neighboring males.

The average height of territory defense was similar for the three most commonly used species (box elder, river birch, and willow), but these three species differed from the others (Tables 14 and 19).

As in feeding, the height of utilization for territorial defense was probably set by the stature of the vegetation, and the low underbrush differs basically because of its small size.

Percentage of time spent defending the territory.--The percentage of time spent defending the territory dropped after the first week of June, then rose slightly during the last of June and the first part of July (Figure 10). A similar trend was also noted in the snow bunting (*Plectrophenax nivalis*) by Tinbergen (1939). After the first week of July the time spent defending the territory dropped off rapidly, but it increased at the end of August, just before migration.

The lines of Figure 10 representing defense activities for 1964 and 1965 (unsprayed) suggested that the levels at the beginning of the observations may have been dropping from a higher percentage from the weeks immediately preceding. This could have been a result of increased singing prior to egg-laying to synchronize reproductive physiology and

Table 19. Average height (in feet) of territorial defense associated with each plant species on a weekly basis

Species of plant	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
						1964							
No. of observations	7	19	26	56	74	102	105	36	--	--	--	--	425
Wild rose	--	--	--	--	--	--	--	6.0	--	--	--	--	6.0
Alder	--	--	--	--	20.0	--	15.0	--	--	--	--	--	16.3
Dogwood	--	--	--	7.0	--	--	--	--	--	--	--	--	7.0
Willow	25.0	25.0	19.1	22.7	19.4	26.1	25.7	25.5	--	--	--	--	22.4
River birch	--	25.0	17.3	25.0	21.4	23.1	20.7	22.5	--	--	--	--	17.4
Box elder	30.0	24.8	26.8	27.6	28.7	26.2	29.0	24.2	--	--	--	--	27.7
All species	28.6	24.9	22.3	24.7	23.7	25.8	27.2	22.4	--	--	--	--	25.2
						1965							
No. of observations	182	99	165	147	121	46	23	14	8	4	30	30	869
Green ash	20.0	--	25.0	--	--	--	--	--	--	--	--	--	22.5
Dogwood	10.0	--	8.0	--	--	--	--	--	--	--	--	--	9.0
River birch	19.1	27.7	21.1	27.0	20.8	29.3	39.2	40.0	8.0	--	30.0	--	24.1
Willow	35.0	30.6	32.1	32.0	33.4	30.0	--	46.3	--	--	35.0	43.6	33.5
Box elder	32.0	31.8	33.7	29.7	33.0	29.8	33.8	45.0	34.3	30.0	34.1	35.3	32.2
All species	31.9	30.4	30.2	30.4	31.9	29.8	35.2	43.9	31.0	30.0	34.0	38.3	31.6

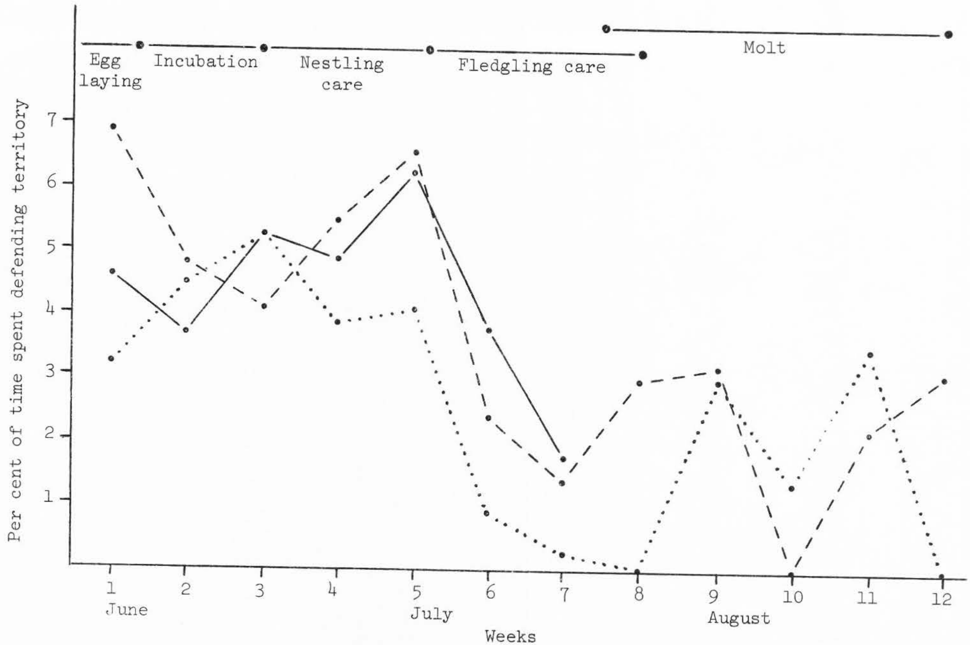


Figure 10. Proportion of the observation time spent defending the territory by the yellow warblers. 1964, solid line; unsprayed 1965, broken line; and sprayed 1965, dotted line.

strengthen the pair-bond as well, as was reported by Verner (1965), studying the marsh wren.

The double peak of increase during August was possibly due to the differential time sequences of stages of the cycle of the individuals, as discussed under feeding height, page 43. This increase represents a revival of song that also was noted in late summer by Saunders (1948).

Individuals from the experimental areas in 1965 spent less time in defense of their territories than did those individuals from the unsprayed areas (Figure 10). This result could have been either a complementary relationship with increased foraging or an actual decrease in territory defense (see Figures 9 and 10).

Summarization of activity

Activities other than foraging or territorial defense were grouped into "other activities" of the birds, which were made up mainly of resting, preening, and (only in early spring) courtship and copulation. The general picture of the resting and maintenance activities paralleled that for territorial defense, both decreasing as the time spent feeding the offspring increased (Figure 11).

An increase in preening during the molt stage might have been expected, but an increase in such activity was not observed (Figure 11). Probably the added physiological needs of feeding fledglings and of molting required the warblers to forage a greater percentage of the time, reducing the time available for preening and resting (compare Figures 9 and 11). Also the amount of time the individual was lost from view increased at this time indicating a more retiring disposition of the birds.

During the experimental phase in 1965 those individuals from the control areas spent a greater percentage of time in resting or in

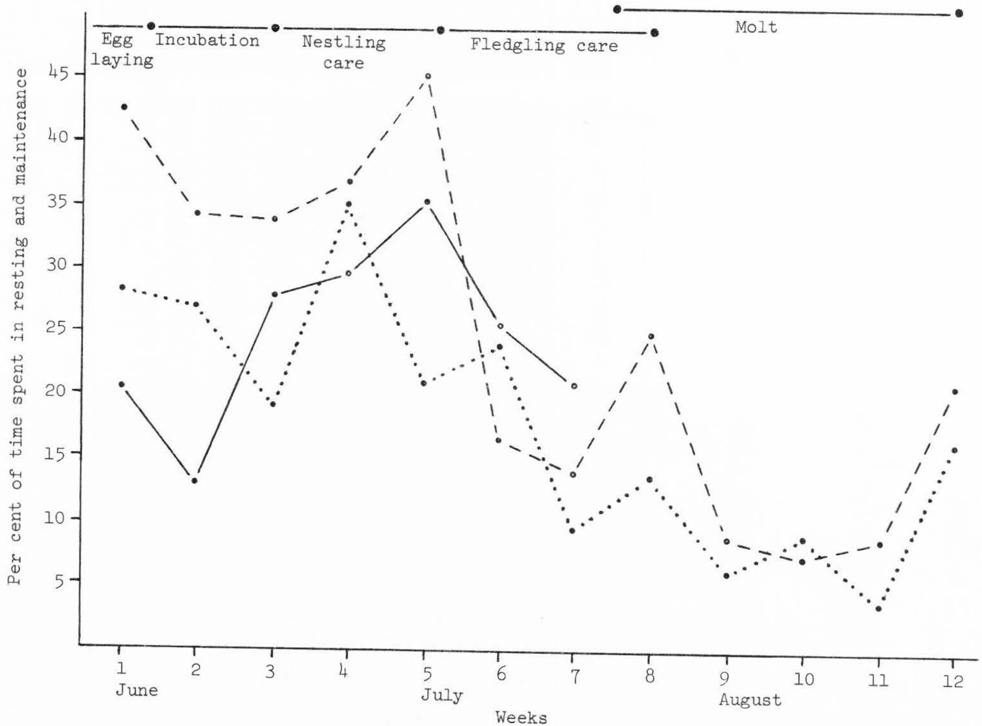
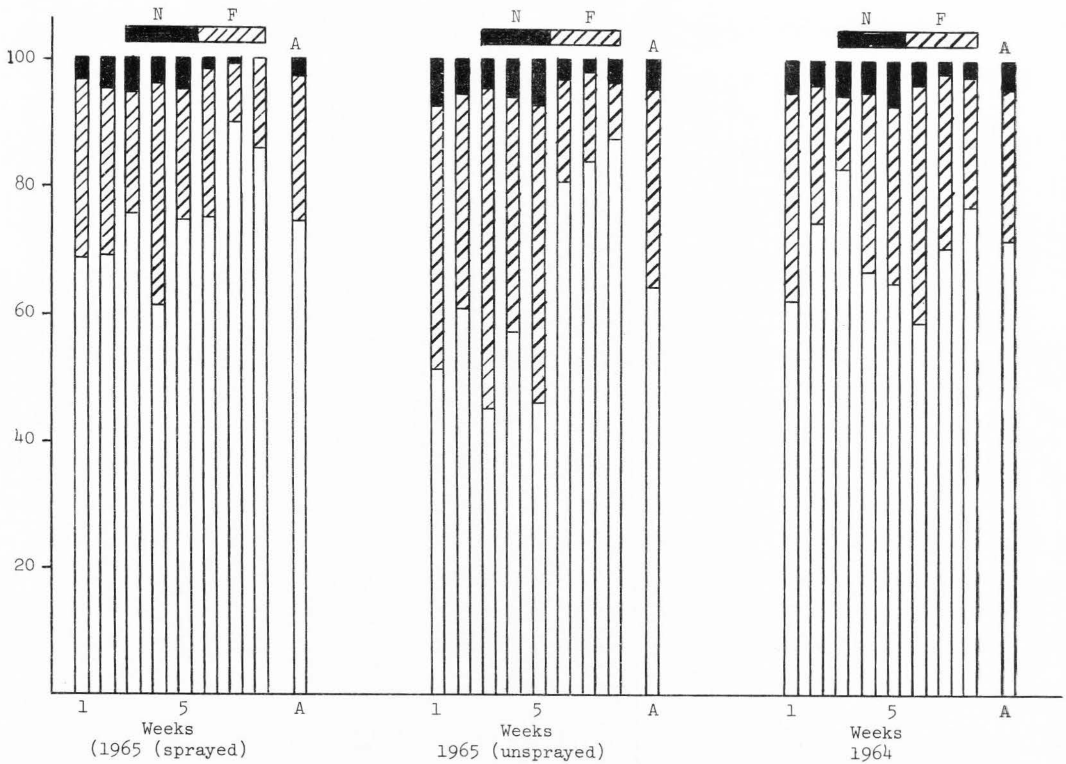


Figure 11. Proportion of the observation time spent in other activities by the yellow warbler. 1964, solid line; unsprayed 1965, broken line; and sprayed 1965, dotted.

maintenance activities than did those individuals from the sprayed territories (Figures 11 and 12). Presumably, the latter were required to spend more time foraging.

The percentage of time spent in each activity appeared to be a complement of the time spent foraging. On the experimental areas the time available for territorial defense, and especially that for resting and plumage care, decreased during the time the insecticide was effective (Figure 12).

The average percentages for defense and for foraging in 1964 and 1965 (unsprayed) were quite comparable, 4.4 and 69.3 versus 4.3 and 64.4. The change in behavior (especially in percentage of time spent feeding) of the birds on the sprayed territories was quite evident, with defense dropping to 3.0 and foraging increasing to 74.2 (Figure 12).


N
F
A
100
80
60
40
20
1
5
A
Weeks
(1965 (sprayed)
1
5
A
Weeks
1965 (unsprayed)
1
5
A
Weeks
1964

DISCUSSION

Habitat and Utilization

A main feature of the habitat of the yellow warbler appears to be proximity to water. However, it is not known why this should be necessary. At no time was any yellow warbler noticed drinking or bathing. A possible reason is that a moist area would produce a more lush vegetation and in turn a greater supply of insects for food items, as suggested by Woodbury and Cottam (1962). Linsdale (1938, p. 119) also noted this situation in central Nevada where

> suitable surroundings were nearly always made up largely of dense, rather tall thickets of willows and rose along with other kinds of plants associated with these. It happened that these thickets often grew close to open water, but apparently this was not part of the requirements of the birds, for they lived in thickets at some places where the ground was only moist, and even where it was completely dry. In the main, though, the moisture was necessary for growth of the plants, and our observations led to the general impression that food supplies for insect-foraging warblers were more abundant in this type of habitat than in the dryer situation.

Bent (1953, p. 203) stated that the yellow warbler does not seem to be attracted to large trees such as cottonwoods, but seems to prefer the more leafy shrubbery and small trees of developmental stages in ecological succession. During this study the larger trees were preferred for most of the summer, with the low underbrush being used less frequently (Tables 11 and 18). The yellow warbler was also noted ranging high in the tops of trees by Grater (1947, p. 66). Almost all of my territories were situated so that they contained a portion of low underbrush, and the difference was not due to the lack of this habitat type. The canopy layer vegetation was utilized more frequently for the greater part of the season, with the low underbrush used more extensively during the fledgling and molt stages. Probably in both cases this more dense vegetation provided better protection from predators.

Griscom and Sprunt (1957, p. 41) stated that the yellow warbler (all subspecies) was a medium- to low-range forager, but they listed no specific heights for their foraging ranges. The present investigation shows conclusively that yellow warblers of the race *morcomi*, associated with the streambank woodland, should be classified as a medium- to high-level forager. They foraged an average of 20 to 25 feet above the ground (Table 14) and many times were recorded feeding in the 40- to 50-foot stratum, and occasionally, 55 feet above the ground. The greatest height of utilization was apparently determined by the height of the canopy.

Most investigators reported heights of nests from 3 to 10 feet; e.g. Bent (1953, p. 203) stated that in *D. p. morcomi* nests generally are placed from 3 to 10 feet above the ground and occasionally as high as 15 feet in the low bushy vegetation (e.g. rosebushes and low willows). During this investigation nest heights from 5 to 30 feet above the ground were recorded. Sixty-five per cent of the 17 nests were in the larger canopy vegetation and only 35 per cent in the low underbrush (Table 20).

Food

Very little information concerning the food of the yellow warbler was found. McAtee (1932) discussed the stomach contents of some 80,000 Nearctic birds, but there was no breakdown to species. The only reference specifically concerning the food of the yellow warblers was that of Kendeigh (1947, p. 38) and was based upon the analysis of only four individuals.

Table 20. Height distribution of yellow warbler nests and per cent utilization according to the species of trees and shrubs

Species	No. of nests	Height in feet			% utilization	
		Max	Min	Mean		
Box elder	7	6	28	19.4		41.2
Willow						
S. melanopsis	4	20	30	24.9	23.6	
S. wolfii	3	7	10	9.0	17.6	
Total	7	7	30	18.0		41.2
Wild rose	3	5	7.5	6.2		17.6
Total	17	5	30	16.5		100.0
Canopy vegetation	11	6	30	21.4	64.7	
Underbrush	6	5	10	7.6	35.3	

Reference has been made to yellow warblers eating food items other than arthropods (mainly insects). Stone (1941) reported twice observing a *D. p. brewsteri* feeding on elderberries in California, and Brooks (1933) stated that yellow warblers, along with Cape May (*D. tigrina*), black-throated green (*D. virens*), and Nashville (*Vermivora ruficapilla*) warblers, pick an occasional grape. During this investigation analysis of 139 stomachs revealed only remains of arthropods, and during all observations no individuals were noted feeding on any of the available fruits and berries, including elderberries, of the area. Possibly those yellow warblers reported to be eating fruits were feeding on insects on the fruits, rather than on the fruits themselves.

The diets of other warblers appear similar to those of the yellow warbler. Nolan (1956) reported spittle insects as food for the prairie warbler (*D. discolor*). Stomach contents of five mourning warblers (*Oporornis philadelphia*) revealed that spiders, various beetles, and Lepidoptera constituted over 50 per cent of the contents (Cox, 1960). In the present investigation these three orders made up only 25.6 and 13.9

per cent of the food items of the yellow warbler in 1964 and 1965, respectively (Table 4). Eyer (1963) observed that insect larvae formed the principal food of the golden-winged warbler (V. chrysoptera) throughout the nestling stage. Other foods brought to the young included large spiders, bugs, and beetles. Martin et al. (1951, p. 163) stated that among insects eaten most commonly by warblers are various kinds of caterpillars, beetles, wasps, ants, fleas, bugs, plant lice, bees, cankerworms, and locusts.

McAtee (1932) stated that Diptera, Hymenoptera, and Coleoptera were utilized as important food items of Nearctic birds. In the study during the spruce budworm outbreak in Ontario Kendeigh (1947) found that Araneida, Homoptera, Coleoptera, and Diptera were taken most frequently by the yellow warbler. In this investigation the five insect orders, Hemiptera, Homoptera, Coleoptera, Diptera, and Hymenoptera, made up 88.2 and 88.3 per cent of the food items of the yellow warbler in 1964 and 1965, respectively (Table 4).

Data from this study showed no preference among arthropods, with the possible exception of Hemiptera in 1965 and Coleoptera in both years. A discussion of possible avoidance of certain orders and the seeming preference of Diptera and Hymenoptera was given in the Results (p. 21). In most cases feeding was probably random, with the yellow warblers taking the food items of appropriate size they found in their search. Stenger (1958), studying the food habits of the ovenbird, reached the same conclusion.

Activities

There have been few intensive studies of the time budgets of a particular species of bird. Some of the more important are those of Hartley (1953), Gibb (1954, 1956), Orians (1961), Root (1964), and Verner (1965).

In the study of the time-energy budgets of the yellow warblers it was shown that the time available for territorial defense and for plumage care and resting were complements of the requirements for foraging (Figure 12). A comparison of foraging activity of the birds from the sprayed and unsprayed territories (where the time values were quite similar to those from 1964) suggests that the reduction of food from approximately 20 per cent of the territory may have forced the birds to devote a greater percentage of their time to foraging. This stress is reflected in the earlier increase in foraging in the nestling stage (Figure 10) on the experimental territories, and in the virtual disappearance of territorial behavior in those territories in late July (Figure 13).

Because of the weight of the yellow warbler (approximately 9.5 grams), there is a large amount of surface area per unit of volume, and the metabolic rate is greater than that of larger species. Salt (1957, p. 385) stated that large birds consume less oxygen and hence require less food per gram of body weight than do small birds, and Gibb (1960) has shown that smaller species tend to spend a longer time foraging than do larger ones. Also, under resting conditions the body temperatures of birds are, on an average, greater than those of mammals (104 to 109 F compared to 98.6 to 102 F). Thus, considerable food is needed to supply enough energy, especially during times of high energy output, such as the feeding of the young and during molt.

Territory

As is apparent through all orders of birds, territory has no single simple, over-all function. Function as used here means reactions tending toward a goal for the conservation and promotion of the species in a qualitative as well as a quantitative sense, as described by Tinbergen (1939). If functions were known for a single species it would be difficult to impute similar territorial functions to other species even in the same family or genus, because of species diversity (Hinde, 1956; Carpenter, 1958; Kuroda, 1960).

Of the postulated functions of territory the question of food value would appear most amenable to quantitative study and/or experimentation. To provide a basis for such study the availability of food was estimated in relation to the food habits of yellow warblers. A food-value index was devised, and this showed that food resources increased essentially in direct proportion to increases in area of the territory. Clearly, food resources did not play a role directly in the determination of territory size in the 17 territories in this study. Beer et al. (1956) also concluded that variability in territory size in the yellow warbler was not determined by a food-value factor. Such a relationship was unexpected in view of results in studies by Stenger (1958), and Gibb (1954, 1956), statements by Tinbergen (1939) and Nice (1941), the five-fold differences in territory size, and conclusions reached by Crook (1965).

Although breeding territories of yellow warblers differed in area by a factor of five, there was apparently a minimum size requirement. Only two of 17 early-season territories were less than 0.2 acre.

A foraging area around the nest is possibly a necessity in this species, since the altricial young require much brooding during the first few days. In this species, having an available food supply near the nest, so that short food-gathering excursions could be made, would be beneficial to survival of the young. This argument was first proposed by Tinbergen (1939), and it seems applicable to the yellow warbler.

In an effort to explore further the size requirements, 20 per cent of the area in each of five experimental territories was sprayed with insecticide. The spraying effected a 30 per cent decrease in food-value index for the four territories on which males survived (Table 5). The index for the four sprayed territories suggests that the birds had on the average only 39 per cent of the available food that existed on the control territories. The activities of males on the sprayed and unsprayed areas were recorded, and time budgets prepared. These comparisons showed a consistent increase in the percentage of time spent in foraging on the sprayed areas and an earlier onset of this foraging increase at the time of nestling care (Figure 9). Comparisons after the time of fledging are less meaningful since (1) the insect populations had recovered and (2) females with some offspring left the territories and were not repulsed by other males. The increase in time spent foraging occurred at the expense of territorial defense, resting, and plumage maintenance (Figure 12).

Despite the induced stress, broods were reared on three of the four experimental areas and a fourth suffered probable human interference just prior to fledging. Thus there appears to be a considerable margin of safety in the food supply, even in the smallest territories. The level of the adjustments suggests, however, that food supply could not have been reduced indefinitely without more serious consequences (especially in years of lower insect population).

However, in years of exceedingly low food availability those yellow warblers holding small territories might modify their behavior. These behavioral adjustments could include increased time spent in foraging, greater amount of trespass, foraging at a different level or on the ground, or foraging off the territory. One such behavioral modification was found by Kendeigh (1941a). The average territory size for D. p. aestiva in northwestern Iowa was about two-fifths of an acre, and many of these birds regularly left their territories to feed in nearby forests. Kendeigh (1941a, p. 173) stated

> where all requirements for nesting are not found [referring to food and possibly singing posts] in any one area, this species [eastern yellow warbler] appears capable of modifying its behavior to make the best of conditions available.

Other functions may bear on territory size. During playback experiments in early May mated males positioned themselves between their mates and the dummy at all times, whenever the females approached the vicinity of the dummy. A tendency was indicated by the male to forcibly keep the female of the territory separated from the intruder, thus discouraging promiscuous mating. Ficken (1962, p. 630) suggested the importance of such aggression in the American redstart (Setophaga ruticilla) and stated "the strong territorial defense exhibited by this species probably reduces the chances of copulation by other males." Those males that cannot defend mates leave fewer offspring. Tompa (1964) noted considerable disruption in reproductive activities of song sparrows by surrounding males in 1962 when there were 17 unmated males compared to 5 in 1961 and 1963. During 1962 Tompa (1964) found the breeding success approximately 40 per cent lower.

Aggressiveness, at least toward simulated intruders, appeared to decrease during the nest-building stage (Figure 10), increasing again at the time of incubation and feeding of nestlings (Table 7). Similar results were noted by Tinbergen (1939), in the snow bunting. However, Stenger (1958) observed a reduction of male song after the eggs hatch in the ovenbird. Figure 10 shows that during incubation and nestling care stages there was approximately a 35 per cent rise in the amount of time spent defending the territory. Also at this time a more aggressive territorial behavior (chasing) was increased (p. 33). This increased aggressiveness at the time of incubation points to isolation that may decrease the chances of disruption of nesting. Presumably a tendency toward more aggressiveness at this stage of the nesting cycle could perpetuate a greater number of progeny per male.

Tompa (1962, 1963, 1964), studying a population of the song sparrow (which normally possesses Hinde's type A territory) on Mandarte Island, off the coast of British Columbia, found that the mean territory size was approximately one-tenth the size of those of the same species on the mainland. In this population the individuals had a common feeding ground in a grassy area off their territories. These individuals still defended their territories, but fed side by side with neighboring males on the grassy area. Even in this situation, pairs with minimum-sized territories reared two or three broods per season. This extreme reduction in size of defended area indicates that territory size is probably not set in accordance with food supply, and that the size normally defended in mainland populations is much greater than necessary for reproductive isolation. Certainly, then, the smallest yellow warbler territories in this study were more than adequate to provide sexual isolation.

The configuration of vegetational boundaries may also be a determinant of territory size, since the warblers sought conspicuous singing perches, often in peripheral foliage at the edge of a clearing. In California, territories of the wrentit (Chamaea fasciata) varied in size from 0.5 to 2.7 acres, and Erickson (1938) showed that these variations were correlated with the length of border which had to be defended against neighbors. This does not appear to be true of the yellow warbler (Figure 13). The correlation of length of border to be defended and territory size was not significant at 0.3. A comparison of the territory size and the footage of open edge area, having no neighboring yellow warblers, failed to demonstrate a correlation between them (Figure 14). In this instance the correlation 0.3 was not significant.

Tinbergen (1939) stated that individual birds differ in many attributes. Some substantiation is provided by studies of the social hierarchy (Allee, 1958) and behavior (Scott, 1958). Conceivably, differences in individual aggressiveness may have played a major role in determination of territory size in this study. The amount of time that each individual yellow warbler male spent defending his territory could be a measure of individual aggressiveness; if this were the case, those individuals that spend more time defending their boundaries should have larger territories. Such a relationship is indicated in Figure 15. There are some deviations from the normal pattern; however, the correlation of territory size to percentage of time spent defending the territory was significant at 0.6.

When associated with sexual jealousy, in present of the female, the male's aggressiveness seemingly increases. The holder of the smallest territory (Table 6), who spent the least amount of time defending his

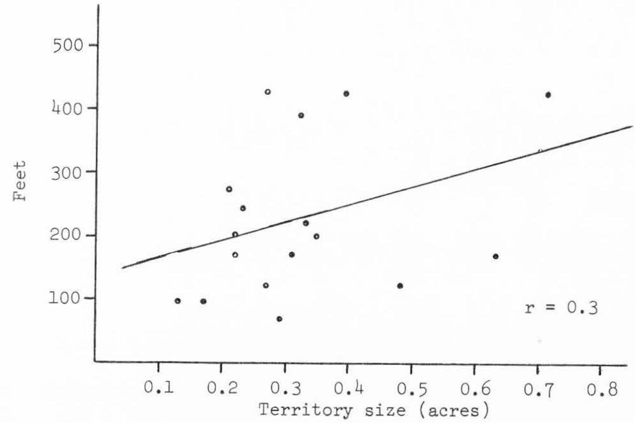


Figure 13. Comparison of the territory size with the length of border to be defended from neighboring males.

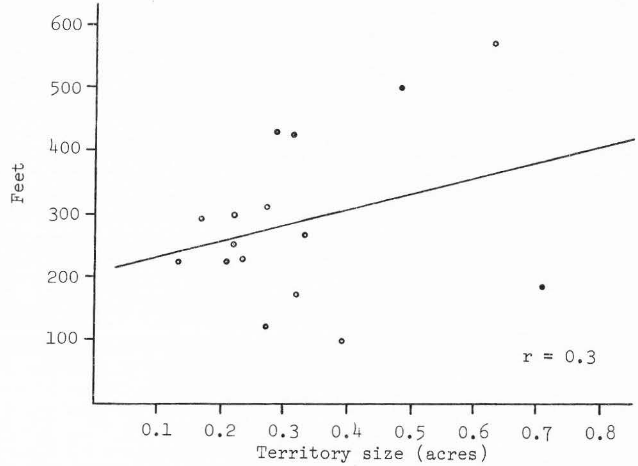


Figure 14. Comparison of the territory size with the length of open edge of the territory.

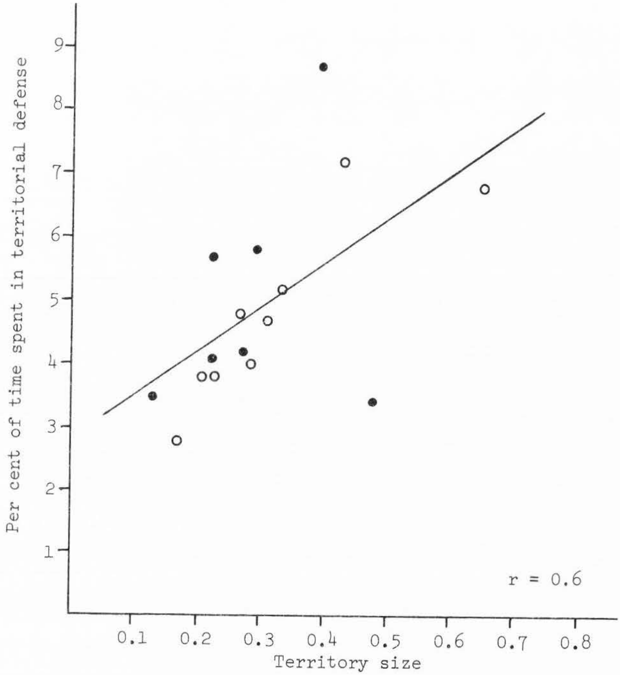


Figure 15. Comparison of the size of the territory with the per cent of time each individual spent defending the territory. , 1964 and o, 1965.

territory, held a territory with almost exactly the same boundaries 3 years in a row. However, when his mate selected a nest site off his territory during the third breeding season (1965), he was able to include the portions containing the nest from an unbanded neighboring bird (Table 6).

This study then indicates that the variation in territory size in the yellow warbler was independent of the provision of an adequate food supply for the pair. Further, the variation was so great that it could not explain the need to provide isolation from conspecifics for reproductive purposes. The variation did not clearly result from the amount of open edge or amount of area to be defended, nor an area for pair isolation. The factor that probably brought about the variation in territory size was that of individual differences in aggressiveness.

SUMMARY AND CONCLUSIONS

The territorial behavior of the yellow warbler was investigated through examination of their food habits, time budgets, and behavioral responses. Particular attention was devoted to the problem of differences in the sizes of territories in relation to food resources available.

The basic habitat of the yellow warbler appeared to be riparian growth, but the presence of water probably was important only because it produced an area where food supplies for insect-foraging warblers were more abundant. Insect availability was low in early June, increasing in the latter part of the summer, from an average of 0.46 to 1.32 grams/1000 grams dried vegetation by late August (Figure 2). This increase of available food resources came during the fledgling stage and reached a peak during the molt stage of the annual cycle.

Stomach contents revealed that arthropods were the only food items eaten by the yellow warbler. Insects made up 98.1 per cent of the diet; the remainder consisted of arachnids. Five orders of insects made up over 88 per cent of the diet. These were Hemiptera, Homoptera, Coleoptera, Hymenoptera, and Diptera. Three methods of foraging were used by the yellow warbler: gleaning, hawking, and hovering. Gleaning was the most common method (94 per cent of observations).

The three basic canopy-forming trees of the habitat (box elder, river birch, and willow) were utilized the greatest proportion of the time for feeding and territory defense. For feeding, a preference was demonstrated for box elder and river birch, and willow appeared to be little used. Samples taken from the three basic trees indicated that box elder and river birch were high insect producers and willow was low. This was true both in biomass and insect families present on the trees.

Feeding heights varied from 1 to 55 feet above the ground, with means from 20 to 25 feet. No significant difference was found in biomass of insects or insect families present in samples from 6, 12, and 24 feet above the ground. The foraging height tended to decrease during the fledgling care and molt stages, when the yellow warblers utilized the low undershrubs. This was probably for protective concealment.

Approximately 70 per cent of the males' time was spent foraging. It appeared that this activity was most important because of physiological needs of the warbler, and its fluctuations affected the percentage of time spent in defending the territory and in other activities (preening and resting). The amount of time spent foraging increased during the fledgling and molt stages, times of greater physiological need.

Spraying with insecticide in 1965 greatly reduced the insect population on the sprayed 20 per cent of five territories (Figure 2), producing a decrease of approximately 30 per cent in the food value of the complete territory. Males from the experimental territories (sprayed) spent more time feeding in comparison to those males of the control territories.

The provision of an adequate food supply for the pair and the young does not explain observed differences in the size of the territory. Territory size was larger than necessary in the 2 years of this study and varied considerably among individuals. Food value was more than adequate and highly variable among territories, the largest value being seven times greater than the smallest, indicating that food probably was a by-product of the territory size. The food-value index was established by taking the seasonal average grams of insects/1000 grams of air-dried vegetation times the diameter of the trees at breast height.

Territory establishment takes place upon arrival of the males in the first part of May. Establishment of the territories was usually evident by the middle of May. First arrivals tended to have larger territories, which were compressed as the yellow warbler density increased. The size of the territories varied from .13 to .65 acres, with the largest territories being five times the size of the smallest. Some change in the location of territory boundaries was noted among the males from the sprayed territories, but this was attributed to choice of nest sites by the females and to the disappearance of one of the males.

The average height of territory defense (25 to 31 feet above the ground) was slightly higher than that for foraging. This was probably a result of some singing alone from high perches. Of the three basic canopy-forming trees of the habitat, box elder and willow appeared to be utilized randomly for territory defense, and river birch was non-preferred.

Males defended their territories by singing, posturing, and chasing. Singing was most commonly used, making up 97 to 99 per cent of the observations. An increased response to playback, an increased percentage of time spent defending the territory, and a more aggressive method of territorial defense (chasing) were prevalent during the late egg-laying and incubation stages of the cycle.

Because of the marked variability in size, an increased response to playback during incubation and nestling care, and increased percentage of time spent defending the territory, and a more aggressive method of territorial defense (chasing), it appears that territory size probably was established in accordance with the aggressiveness of each male, thus establishing an area more than large enough for pair isolation and, incidentally, a territory more than large enough to supply ample food for the pair and their young. There was no significant correlation between territory size and territory edge defended against neighboring males or the length of territory open edge where common boundaries were not present.

The above-mentioned data on playback and territory defense indicate that a factor of more importance than defense of an adequate food supply for the pair and young was isolation of the pair from other members of the same species to reduce interference during reproductive activities. Food being available near the nest during the first few days of the nestling stage was possibly important.

LITERATURE CITED

Allee, W. C. 1958. The social life of animals. Beacon Press, Beacon Hill, Boston. 233 p.

Armstrong, E. A. 1965. Bird display and behaviour. Dover Publications, Inc., New York. 431 p.

Beer, J. R., L. D. Frenzel, and N. Hansen. 1956. Minimum space requirements of some nesting passerine birds. Wilson Bull. 68:200-209.

Bent, A. C. 1953. Life histories of North American wood warblers. U. S. Nat. Museum Bull. 203. Washington, D. C.

Borror, D. J. and D. M. DeLong. 1964. An introduction to the study of insects. Holt, Rinehart and Winston, New York. VII. 819 p.

Brooks, M. 1933. Cape May warblers destructive to grapes. Auk 50:222-223.

Carpenter, C. R. 1958. Territoriality: A review of concepts and problems, p. 224-250. In A. Roe and G. G. Simpson, eds. Behavior and evolution. Yale Univ. Press, New Haven, Conn.

Cox, G. W. 1960. A life history of the mourning warbler. Wilson Bull. 72:5-28.

CRAG Agricultural Chemicals. 1961. Summary of technical information, Sevin (insecticide). Long Island City, New York, S-TI, F-40732. 24 p.

Crook, J. H. 1965. The adaptive significance of avian social organization, p. 181-218. In P. E. Ellis, ed. Social organization of animal communities. Symp. Zool. Soc. London, Academic Press, New York.

Erickson, M. M. 1938. Territory, annual cycle and numbers in a population of wren-tits (*Chamaea fasciata*). Univ. Calif. Publ. Zool. 42:247-334.

Eyer, L. E. 1963. Observations on golden-winged warblers at Itasca State Park, Minnesota. Jack-Pine Warbler 41:96-109.

Ficken, M. S. 1962. Agonistic behavior and territory in the American redstart. Auk 79:607-632.

Ficken, M. S. and R. W. Ficken. 1962. The comparative ethology of the wood warblers: a review, p. 103-122. In O. S. Pettingill Jr., ed. The living bird. The Laboratory of Ornithology at Cornell Univ., New York.

Frydendall, M. J. Postnuptial molt cycle of the yellow warbler. Manuscript.

Gibb, J. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96:513-543.

Gibb, J. 1956. Food, feeding habits and territory of the rock pipit Anthus spinoletta. Ibis 98:506-530.

Gibb, J. A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis 102:163-208.

Gibb, J. and M. M. Betts. 1958. Predation by birds on forest insects. Int. Union of Forest Res. Org., 12th Congress, Oxford 1956, Papers, 2(24):204-208.

Grater, R. K. 1947. Birds of Zion, Bryce, and Cedar Breaks. Zion-Bryce Mus. Bull., No. 5. 98 p.

Griscom, L. and A. Sprunt, Jr. 1957. The warblers of America. The Devin-Adair Co., New York. 356 p.

Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. Jour. Anim. Ecol. 22:261-288.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

Holmgren, A. H. 1965. Handbook of the vascular plants of the Northern Wasatch. National Press, Palo Alto, Calif. 202 p.

Howard, H. E. 1920. Territory in bird life. Murray, London.

Kendeigh, S. C. 1941a. Birds of a prairie community. Condor 43:165-174.

Kendeigh, S. C. 1941b. Territorial and mating behavior of the house wren. Ill. Biol. Monog. 18:1-120.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Biol. Bull., Dept. Lands and Forests 1:1-100.

Koersveld, E. von. 1950. Difficulties in stomach analysis. Proc. X Int. Ornithol. Congr. 592-594.

Kuroda, N. 1960. An essay on bird territoriality. Misc. Reports Yamashinas Inst. for Ornith. and Zool. 2:133-137.

Lack, D. 1948. Notes on the ecology of the robin. Ibis 90:252-279.

Lack, D. 1954. The natural regulation of animal numbers. The Clarendon Press, Oxford. 343 p.

Lewis, H. F. 1939. Reverse migration. Auk 56:13-27.

Linsdale, J. M. 1938. Environmental responses of vertebrates in the Great Basin. Amer. Midl. Nat. 19:1-206.

McAtee, W. L. 1932. Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the foods of nearctic birds. Smithsonian Misc. Collections 85(7):1-201.

Martin, A. C., H. S. Zim., and A. L. Nelson. 1951. American wildlife and plants. McGraw-Hill Book Co., Inc., New York. 500 p.

Mayr, E. 1935. Bernard Altum and the territory theory. Proc. Linnaean Soc. New York 45-46:15 p.

Mickey, F. W. 1943. Breeding habits of McCown's longspurs. Auk 60:181-209.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat. 26:441-487.

Nolan, V., Jr. 1956. Spittle insects as food or prairie warblers. Auk 73:557.

Orians, G. H. 1961. The ecology of blackbirds (Agelaius) social systems. Ecol. Monog. 31:285-312.

Root, R. B. 1964. Ecological interactions of the chestnut-backed chickadee following a range extension. Condor 66:229-238.

Salt, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373-393.

Saunders, A. A. 1948. The seasons of bird song. Revival of song after post-nuptial molt. Auk 65:373-383.

Schrantz, F. G. 1943. Nest life of the eastern yellow warbler. Auk 60: 367-387.

Scott, J. P. 1958. Animal behavior. Univ. of Chicago Press, Chicago, Ill. 281 p.

Snedecor, G. W. 1956. Statistical methods. Iowa State Univ. Press, Ames, Iowa. p. 534.

Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. Auk 75:335-346.

Stone, N. W. 1941. Elderberries as food for birds. Condor 43:121.

Sutton, G. M. and D. F. Parmelee. 1955. Summer activities of the lapland longspur of Baffin Island. Wilson Bull. 67:110-127.

Tinbergen, N. 1939. The behavior of the snow bunting in spring. Trans. Linn. Soc. N. Y. 5:1-94.

Tompa, F. S. 1962. Territorial behavior: the main controlling factor of a local song sparrow population. Auk 79:687-697.

Tompa, F. S. 1963. Behavioral response of song sparrows to different environmental conditions. Proc. XIII Int. Ornithol. Congr. 729-739.

Tompa, F. S. 1964. Factors determining the numbers of song sparrows, Melospiza melodia (Wilson), on Mandarte Island, B. C., Canada. ACTA Zoologica Fennica 109:1-73.

Verner, J. 1965. Time budgets of the male long-billed marsh wren during the breeding season. Condor 67:125-139.

Weeden, J. (Stenger) and J. B. Falls. 1959. Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343-351.

Woodbury, A. M. and C. Cottam. 1962. Ecological studies of birds in Utah. Univ. of Utah Biol. Series 12(7):1-33.

APPENDIXES

APPENDIX A

Table 21. Feeding method associated with all species of plants utilized in 1965 (unsprayed territories), expressed as per cent. Gl T L, gleaning on terminal leaves; Gl B, gleaning on bole.

Species of plant	Feeding method	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Wild rose	Gl T L	--	--	--	--	--	--	--	--	--	--	100.0	--	100.0
Dogwood	Hover	--	--	--	--	--	--	22.2	--	--	--	--	--	18.2
	Gl T L	--	--	--	--	--	--	77.8	--	--	100.0	100.0	--	81.8
Hawthorn	Gl T L	--	--	--	--	--	--	100.0	--	--	--	--	--	100.0
Green ash	Gl T L	100.0	--	100.0	--	--	--	--	--	--	--	--	--	100.0
River birch	Hover	--	6.7	--	--	--	--	3.4	--	--	--	--	--	1.5
	Hawk	5.0	13.3	--	--	--	--	--	--	--	--	--	--	2.2
	Gl B	15.0	6.7	--	8.4	--	--	--	--	--	--	--	--	3.6
	Gl T L	80.0	73.3	100.0	91.6	100.0	100.0	96.6	100.0	100.0	--	100.0	100.0	92.7
Willow	Hover	--	--	--	12.5	--	--	--	--	--	--	--	--	1.0
	Hawk	--	--	--	--	--	--	4.0	--	--	--	--	--	1.0
	Gl T L	100.0	100.0	100.0	87.5	100.0	100.0	96.0	100.0	--	100.0	100.0	100.0	98.0
Box elder	Hover	1.7	--	--	1.6	4.1	3.0	--	7.7	--	--	--	--	1.6
	Hawk	--	--	--	--	--	1.5	--	--	--	--	--	6.2	0.7
	Gl T L	98.3	100.0	100.0	98.4	95.9	95.5	100.0	92.3	100.0	100.0	100.0	93.8	97.7
Total	Hover	1.0	1.6	--	2.4	3.8	2.4	3.1	4.3	--	--	--	--	1.7
	Hawk	1.0	3.2	--	--	--	1.1	1.0	--	--	--	--	4.9	1.0
	Gl B	3.0	1.5	--	1.2	--	--	--	--	--	--	--	--	0.7
	Gl T L	95.0	93.7	100.0	96.4	96.2	96.5	95.9	95.7	100.0	100.0	100.0	95.1	96.5

Table 22. Feeding method associated with all species of plants utilized in 1965 (sprayed territories), expressed as per cent. Gl T L, gleaning on terminal leaves; Gl B, gleaning on bole

Species of plant	Feeding method	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Dogwood	Gl T L	--	--	100.0	--	--	--	100.0	100.0	--	--	--	100.0	100.0
Wild rose	Gl T L	--	--	--	--	--	--	100.0	--	--	--	100.0	100.0	100.0
River birch	Hover	--	14.3	16.7	12.5	--	--	7.1	--	--	--	--	--	6.5
	Hawk	--	4.8	--	--	--	5.3	14.3	--	--	--	--	--	3.2
	Gl B	33.3	9.5	--	12.5	12.5	15.8	14.3	25.0	--	--	--	--	10.5
	Gl T L	66.7	71.4	83.3	75.0	87.5	78.9	64.3	75.0	100.0	--	--	--	79.8
Willow	Hover	3.5	--	2.4	4.5	3.8	4.4	--	--	--	--	--	--	2.2
	Hawk	7.1	20.0	2.4	--	--	4.4	--	--	--	--	--	--	2.3
	Gl T L	89.3	80.0	95.2	95.5	96.2	91.2	100.0	100.0	--	--	100.0	100.0	95.5
Box elder	Hover	--	--	2.0	8.2	3.8	13.9	5.3	--	--	--	--	--	4.4
	Hawk	--	2.3	2.0	--	--	2.8	--	--	--	--	--	--	1.3
	Gl T L	100.0	97.7	96.0	91.8	96.2	83.3	94.7	100.0	100.0	100.0	100.0	100.0	94.3
Total	Hover	1.1	4.0	4.5	7.7	2.9	7.7	4.1	--	--	--	--	--	4.1
	Hawk	2.2	5.3	1.8	--	--	3.9	2.1	--	--	--	--	--	1.9
	Gl B	1.1	2.7	--	1.1	2.9	3.8	2.0	3.4	--	--	--	--	1.9
	Gl T L	95.6	88.0	93.7	91.2	94.2	84.6	91.8	96.6	100.0	100.0	100.0	100.0	92.1

Table 23. The per cent utilization of each species of tree, sprayed and unsprayed territories, 1965

Species of vegetation	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Total
Sprayed territories													
Wild rose	--	--	--	--	--	--	3.1	--	--	--	3.5	9.5	0.8
Dogwood	--	--	0.9	--	--	--	1.0	3.4	--	--	--	4.8	0.5
River birch	3.3	28.0	16.2	8.8	23.5	24.4	14.3	13.8	48.1	--	--	--	16.3
Willow	30.4	13.3	37.8	24.2	25.5	29.5	23.5	55.2	--	--	31.0	38.1	27.2
Box elder	65.2	57.3	45.1	67.0	51.0	46.1	58.2	27.6	51.9	100.0	65.5	47.6	54.9
Unsprayed territories													
Wild rose	--	--	--	--	--	--	--	--	--	--	4.4	--	0.3
Dogwood	--	--	--	--	--	--	9.3	--	--	6.7	2.2	--	1.6
Hawthorn	--	--	--	--	--	--	3.1	--	--	--	--	--	0.4
Green ash	2.0	--	2.7	--	--	--	--	--	--	--	--	--	0.6
River birch	20.0	23.8	18.1	14.5	5.6	16.5	29.8	26.1	92.9	--	15.6	9.7	19.7
Willow	19.0	14.3	11.1	9.6	1.9	5.9	23.8	17.4	--	20.0	24.5	12.2	14.2
Box elder	59.0	61.9	68.1	75.9	92.5	77.6	32.0	56.5	7.1	73.3	53.3	78.1	63.2

Table 24. Mean feeding heights associated with each plant species, sprayed and unsprayed territories, 1965

Species of vegetation	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Total
						Sprayed territories							
Wild rose	--	--	--	--	--	--	2.7	--	--	--	3.0	3.5	3.0
Dogwood	--	--	8.0	--	--	--	5.0	10.0	--	--	--	6.0	7.3
River birch	13.3	18.3	25.6	17.1	18.0	16.8	23.9	10.8	7.3	--	--	--	18.1
Willow	26.6	16.5	23.5	18.4	15.9	16.8	13.6	3.1	--	--	10.7	6.5	17.4
Box elder	30.8	32.0	31.4	24.6	26.9	17.6	21.2	16.3	25.0	27.9	30.8	14.3	26.2
Average	29.1	26.0	27.3	22.4	22.0	17.2	19.1	8.0	16.3	27.9	23.6	9.9	22.3
						Unsprayed territories							
Wild rose	--	--	--	--	--	--	--	--	--	--	4.5	--	4.5
Dogwood	--	--	--	--	--	--	8.3	--	--	5.0	6.0	--	7.8
Hawthorn	--	--	--	--	--	--	9.3	--	--	--	--	--	9.3
Green ash	20.0	--	25.0	--	--	--	--	--	--	--	--	--	22.5
River birch	24.3	31.3	26.2	24.6	15.0	27.1	22.6	33.3	20.8	--	26.4	32.5	25.4
Willow	35.8	22.7	38.1	18.8	15.0	23.0	12.5	37.5	--	13.3	11.0	35.6	23.2
Box elder	30.6	32.3	31.8	46.2	32.9	27.8	29.9	36.2	45.0	35.0	24.8	36.9	33.4
Average	30.1	30.7	32.7	40.4	31.5	27.4	20.6	35.7	22.5	28.7	20.3	36.2	29.7

APPENDIX B

Table 25. Proportions of the observations for each species of plant utilized for the different methods of territorial defense for 1965, for sprayed and unsprayed territories, expressed as per cent

Species of vegetation	Terr. defense type	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Total
						Sprayed territories								
Dogwood	Singing	-	-	100.0	-	-	-	-	-	-	-	-	-	100.0
River birch	Chasing	-	-	-	-	-	-	-	-	100.0	-	-	-	3.1
	Singing	100	100	100.0	100.0	100.0	-	-	-	-	-	-	-	96.9
Willow	Chasing	-	-	-	4.0	16.7	-	-	-	-	-	-	-	2.5
	Singing	100	100	100.0	96.0	83.3	100	-	-	-	-	-	-	97.5
Box elder	Singing	100	100	100.0	100.0	100.0	100	100.0	-	100.0	100	100	-	100.0
All species	Chasing	-	-	-	1.5	3.3	-	-	-	14.3	-	-	-	1.0
	Singing	100	100	100.0	98.5	96.7	100	100.0	-	85.7	100	100	-	99.0
						Unsprayed territories								
Dogwood	Singing	100	-	-	-	-	-	-	-	-	-	-	-	100.0
Green ash	Singing	100	-	100.0	-	-	-	-	-	-	-	-	-	100.0
River birch	Chasing	-	-	-	-	-	-	16.7	-	-	-	-	-	1.6
	Singing	100	100	100.0	100.0	100.0	100	83.3	100	-	-	100	-	98.4
Willow	Chasing	-	-	6.2	-	5.9	-	-	-	-	-	-	-	1.5
	Singing	100	100	93.8	100.0	94.1	100	-	100	-	-	100	100	98.5
Box elder	Singing	100	100	100.0	100.0	100.0	100	100.0	100	100.0	-	100	100	100.0
All species	Chasing	-	-	1.3	-	1.7	-	5.3	-	-	-	-	-	0.6
	Singing	100	100	98.7	100.0	98.3	100	94.7	100	100.0	-	100	100	99.4

Table 26. The per cent utilization of each plant species for territorial defense, 1965, sprayed and unsprayed territories

Species of vegetation	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Sprayed territories													
Dogwood	--	--	1.1	--	--	--	--	--	--	--	--	--	0.3
River birch	1.3	10.9	14.3	1.5	16.4	--	--	--	14.3	--	--	--	8.0
Willow	36.0	21.8	45.0	36.7	19.7	41.7	--	--	--	--	--	--	30.5
Box elder	62.7	67.3	39.6	61.8	63.9	58.3	100.0	--	85.7	100.0	100.0	--	61.2
Unsprayed territories													
Dogwood	0.9	--	--	--	--	--	--	--	--	--	--	--	0.2
Green ash	0.9	--	1.4	--	--	--	--	--	--	--	--	--	0.4
River birch	15.0	15.9	20.3	5.1	3.3	20.6	31.6	28.6	--	--	7.7	--	13.1
Willow	45.8	36.4	21.5	22.7	28.4	14.7	--	28.6	--	--	7.7	36.7	28.8
Box elder	37.4	47.7	56.8	72.2	68.3	64.7	68.4	42.8	100.0	--	84.6	63.3	57.5

Table 27. Average height of territorial defense associated with each plant species for 1965, sprayed and unsprayed territories

Species of vegetation	Weeks (June) 1	2	3	4	(July) 5	6	7	8	(August) 9	10	11	12	Average
Sprayed territories													
Dogwood	--	--	8.0	--	--	--	--	--	--	--	--	--	8.0
River birch	20.0	20.0	27.3	20.0	20.0	--	--	--	8.0	--	--	--	19.2
Willow	32.0	25.8	29.2	23.4	25.3	26.0	--	--	--	--	--	--	27.0
Box elder	33.1	31.6	32.6	26.0	29.4	24.3	27.5	--	32.5	30.0	32.1	--	29.9
Average	32.5	29.1	30.2	24.9	27.1	25.0	27.5	--	29.0	30.0	32.1	--	28.7
Unsprayed territories													
Dogwood	10.0	--	--	--	--	--	--	--	--	--	--	--	10.0
Green ash	20.0	--	25.0	--	--	--	--	--	--	--	--	--	22.5
River birch	19.1	34.3	29.7	28.8	25.0	29.3	39.2	40.0	--	--	30.0	--	30.6
Willow	36.6	34.1	39.4	43.9	39.1	34.0	--	46.3	--	--	35.0	43.6	39.1
Box elder	30.7	32.1	34.5	32.9	36.3	31.6	35.8	45.0	45.0	--	37.3	35.3	36.1
Average	31.4	33.2	34.5	35.2	36.8	31.5	36.8	43.9	45.0	--	36.5	38.3	36.7