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POPULATION ECOLOGY OF SOME WARBLERS OF NORTHEASTERN CONIFEROUS FORESTS[1]

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INTRODUCTION

Five species of warbler, Cape May (*Dendroica tigrina*), myrtle (*D. coronata*), black-throated green (*D. virens*), blackburnian (*D. fusca*), and bay-breasted (*D. castanea*), are sometimes found together in the breeding season in relatively homogeneous mature boreal forests. These species are congeneric, have roughly similar sizes and shapes, and all are mainly insectivorous. They are so similar in general ecological preference, at least during years of abundant food supply, that ecologists studying them have concluded that any differences in the species' requirements must be quite obscure (Kendeigh, 1947; Stewart and Aldrich, 1952). Thus it appeared that these species might provide an interesting exception to the general rule that species either are limited by different factors or differ in habitat or range (Lack, 1954). Accordingly, this study was undertaken with the aim of determining the factors controlling the species' bundances and preventing all but one from being exterminated by competition.

LOGICAL NATURE OF POPULATION CONTROL

Animal populations may be regulated by two types of events. The first type occurs (but need not exert its effect) independently of the density of the population. Examples are catastrophes

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such as storms, severe winters, some predation, and some disease. The second type of event depends upon the density of the population for both its occurrence and strength. Examples are shortages of food and nesting holes. Both types seem to be important for all well-studied species. The first kind will be called density independent and the second density dependent. This is slightly different from the usual definitions of these terms which require the effects upon the population and not the occurrence to be density independent or dependent (Andrewartha and Birch 1954).

When density dependent events play a major role in regulating abundance, interspecific relations are also important, for the presence of an individual of another species may have some of the effects of an individual of the original density dependent species. This is clearly illustrated by the generalized habitats of the few species of passerine birds of Bermuda contrasted with their specialized habitats in continental North America where many additional species are also present (Bourne 1957).

If the species' requirements are sufficiently similar, the proposition of Volterra (1926) and Gause (1934), first enunciated by Grinnell (1922), suggests that only one will be able to persist, so that the existence of one species may even control the presence or absence of another. Because of this proposition it has become customary for ecologists to look for differences in food

or habitat of related species; such differences, if found, are then cited as the reason competition is not eliminating all but one of the species. Unfortunately, however, differences in food and space requirements are neither always necessary nor always sufficient to prevent competition and permit coexistence. Actually, to permit coexistence it seems necessary that each species, when very abundant, should inhibit its own further increase more than it inhibits the other's. This is illustrated in Figure 1. In this figure, the populations of the two species form the coordinates so that any point in the plane represents a population for each species. Each shaded area covers the points (i.e., the sets of combined populations of the species) in which the species corresponding to the shading can increase, within a given environment. Thus, in the doubly-shaded area both species increase and in the unshaded area both species decrease. The arrows, representing the direction of population change, must then be as shown in the figure for these regions. In order that a stable equilibrium of the two species should exist, the arrows in the singly shaded regions obviously must also be as in the figure; an interchange of the species represented by the shading would reverse the directions of these arrows resulting in a situation in which only one species could persist. Thus, for stability, the boundaries of the shaded zones of increase must have the relative slope illustrated in the figure with each species inhibiting its own further increase more than the other's. The easiest way for this to happen would be to have each species' population limited by a slightly different factor. It is these different limiting factors which are the principal problem in an investigation of multispecific animal populations regulated by density dependent events.
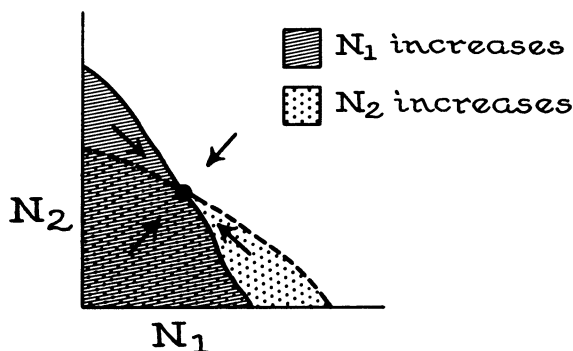

FIG. 1. The necessary conditions for a stable equilibrium of two species. The coordinate axes represent the populations of the species.

An example which has not received sufficient attention is competition in a heterogeneous en-

vironment. As has often been pointed out (Kluijver and Tinbergen 1953, Lack 1955, Hinde 1956) birds may emigrate or disperse from the most suitable areas where reproduction is successful into marginal habitats. Consider such a species which will be called A. Let B be a species that lives only in the area that is marginal for species A. Now, even if in an unlimited environment of this type, species B would eliminate species A by competition, in the heterogeneous environment species B may be eliminated from its own preferred habitat. For, if there is sufficient dispersal by species A, it may maintain, partly by immigration, such a high population in the marginal habitat that species B is forced to decrease. This process is probably very important in considering the environmental distributions of birds and implies that small areas of habitat typical for one species may not contain that species.

The study of limiting factors in nature is very difficult because ideally it requires changing the amount of the factor alone and observing whether this change affects the size of the population. Theoretically, if more than one factor changes, the analysis can still be performed, but in practice, if more changes of known nature occur, more of an unknown nature usually also occur. Limiting factors have been studied in two ways. The best way is artificially to modify single factors in the environment, observing the effect upon the birds. MacKenzie (1946) reviews some experiments of this type. The most notable was the increase from zero to abundant of pied flycatchers (Muscicapa hypoleuca) when nest boxes were introduced in the Forest of Dean. This showed conclusively that lack of nesting sites had limited the population. Such simple modifications are not always feasible. For instance, changing the food supply of an insectivorous bird is nearly impossible. The most feasible approach in such a case is to compare the bird populations in two regions which differ in the abundance of the factor being considered. Ideally, the two regions should differ only in this respect, but this is very improbable. A good example of this method of study is the work of Breckenridge (1956) which showed that the least flycatchers (Empidonax minimus) were more abundant in a given wood wherever the wood was more open.

The present study of the factors limiting warblers was conducted by the second approach. This is slightly less accurate than the first method, but permits studying more factors and requires less time. There are actually four parts to the study. First, it is shown that density dependent events play a large role in controlling the populations of

the species. Second, a discussion of the general ecology of the species (food, feeding zones, feeding behavior, territoriality, predators, and mortality) is presented. The observations were made in the summers of 1956 and 1957. Third, the habits of the different species in different seasons are compared to see what aspects of the general ecology are invariant and hence characteristic of the species. Some observations on the species' morphology are discussed in the light of these characteristics. This was the project of the fall and winter of 1956 and the spring of 1957. Finally, a wood-to-wood comparison of species abundances, relative to the important constituents of their niches as determined in the earlier stages, is presented. This work was done in the summers of 1956 and 1957.

DENSITY DEPENDENCE

It is the aim of this section to demonstrate that the five species of warbler are primarily regulated by density dependent events, that is, that they increase when rare and decrease when common (relative to the supply of a limiting factor). The strongest argument for this is the correlation of abundances with limiting factors discussed later. However, to avoid any risk of circularity, an independent partial demonstration will now be given.

If density independent events do not occur randomly but have a periodic recurrence, then a population controlled by these events could undergo a regular oscillation nearly indistinguishable in form from that of a population regulated by density dependent events. The distinction can be made, however, by observing the effect of the presence of an ecologically similar species. Here it will first be shown that increases and decreases are not random; then an argument will be given which renders the density independent explanation improbable.

If increases, I, and decreases, D, occur randomly, the sequence of observed I's and D's would have random order. A run of I's (or D's) is a sequence (perhaps consisting of one element) of adjacent I's (or D's) which cannot be lengthened; i.e., the total number of runs is always one greater than the number of changes from I to D or D to I. If more runs of I's or D's are observed than would be expected in a random sequence, then an increase makes the following change more likely to be a decrease and conversely. This is what would be expected on the hypothesis of density dependent events.

There have been very few extensive censuses of any of the five species of warbler that are studied here. The longest are reproduced below

from the data of Smith (1953) in Vermont, Williams (1950) in Ohio, and Cruickshank (1956) in Maine. The populations of myrtle, black-throated green, and blackburnian are listed; only those species are mentioned that are consistently present.

Myrtle
| Maine | 7 | 5 | 7 | 7 | 6 | 7 | 8 | 10 | 9 | 8 | 10 | 10 | 10 |
| | | 8 | 10 | 7 | 10 | | | | | | | | |

Black-throated green
Ohio	3	3	5	3	4	3	2	4	0	1	–	3	3
			3	4	3	3	4	3					
Vermont	7	7	7	6	8	5	6	6	7	8	8	6	8
			8	3	6	3							
Maine	8	9	11	10	10	10	11	11	11	10	11	9	8
			9	8	9								

Blackburnian
Vermont	11	11	10	7	8	7	7	10	10	8	5	6	3
			3	6	6	5							
Maine	2	4	3	3	5	5	7	5	6	5	7	5	5
			7	6	6	3							

The increases, I, and decreases, D, of these censuses, in order are as follows:

Myrtle
D I D I I I D D I D I D I

Black-throated green
I D I D D I D I I I D I D
D I D I I I D I D I D
I I D I D I D D I D I

Blackburnian
D D I D I D D I D I D
I D I I D I D I D I D D

In this form the data from different censuses are perfectly compatible and, since censuses end or begin with I or D in no particular pattern, all the censuses for a given species may be attached:

Myrtle
<u>D</u> <u>I</u> <u>D</u> <u>I I I</u> <u>D D</u> <u>I</u> <u>D</u> <u>I</u> <u>D</u> <u>I</u>   (10)

Black-throated green
<u>I</u> <u>D</u> <u>I</u> <u>D D</u> <u>I</u> <u>D</u> <u>I I I</u> <u>D</u> <u>I</u> <u>D D</u> <u>I</u> <u>D</u>

<u>I I I</u> <u>D</u> <u>I</u> <u>D</u> <u>I</u> <u>D</u> <u>I I</u> <u>D</u> <u>I</u>   (27)

<u>D</u> <u>I</u> <u>D D</u> <u>I</u> <u>D</u> <u>I</u>

Blackburnian
<u>D D</u> <u>I</u> <u>D</u> <u>I</u> <u>D D</u> <u>I</u> <u>D</u> <u>I</u> <u>D</u> <u>I</u> <u>D</u> <u>I I</u> <u>D</u> <u>I</u>

<u>D</u> <u>I</u> <u>D</u> <u>I</u> <u>D D</u>   (19)

Here the groups of letters underlined are runs and the number of runs is totalled in parentheses. From the tables of Swed and Eisenhart (1943), testing the one-sided hypothesis that there are no more runs than would be expected by chance, each of these shows a significantly large number of runs (the first less than 5% significance, the others less than 2.5%). That is, each species tends to decrease following an increase and to increase following a decrease, proving population control non-

random. The mean periods of these fluctuations can easily be computed. For a run of increases followed by a run of decreases constitutes one oscillation. Thus, the periods of the oscillations of the three species are $13/5 = 2.6$, $70/27 = 2.6$, and $46/19 = 2.4$ years respectively. These fluctuations would require an unknown environmental cycle of period approximately 2.5 years if a regularly recurring density independent event were controlling the populations. Thus, from these data alone, it seems very probable that the three species (myrtle, black-throated green, blackburnian) are primarily regulated by density dependent events.

A species may be regulated by density dependent events and yet undergo dramatic changes in populations due to changes in the limiting factor itself. In this case tests by the theory of runs, used above, are likely to be useless. However, if a correlation can be made of the population with the environmental factor undergoing change, then not only can density dependence, i. e. existence of a limiting factor, be established, but also the nature of the limiting factor. For, if an increase in one environmental variable can be established, an experiment of the first type described above has been performed. That is, the habitat has been modified in one factor and a resulting change in bird population has been observed. Therefore, because the population changes, that one factor has been limiting.

This is apparently what happens in populations of Cape May and bay-breasted warblers. Kendeigh (1947), examining older material, established the fact that these species are abundant when there is an outbreak of Choristoneura fumiferana (Clem.), the spruce budworm. More recent information confirms this. To correlate with the fact (Greenbank 1956) that there have been continuously high budworm populations since 1909, there is the statement of Forbush (1929) that the Cape May warbler became more common about 1909, and the statement of Bond (pers. comm.) that the winter range of the species has been increasing in size. An outbreak of spruce budworms started in northern Maine in the late 1940's, and Stewart and Aldrich (1951) and Hensley and Cope (1951) studied the birds during 1950 and 1951. Cape May and bay-breasted warblers were among the commonest birds present, as in the earlier outbreaks, although both species were formerly not common in Maine (Knight 1908). The outbreak has continued through New Brunswick, where current bird studies (Cheshire 1954) indicate that bay-breasted is again the commonest bird, although

for unknown reasons the Cape May has not been observed.

In conclusion, it appears that all five species are primarily regulated by density dependent events, and that a limiting factor is food supply for bay-breasted and Cape May warblers.

GENERAL ECOLOGY

The density dependence tentatively concluded above implies that the presence of individuals of a species makes the environment less suitable for other individuals of that species. It would also be expected then that the presence of individuals of one species may make the environment less suitable for individuals of a different species. This is called interspecific competition. As mentioned above, this seems to mean that two sympatric species will have their populations limited by different factors so that each species inhibits its own population growth more than it inhibits that of the others. The factors inseparably bound to a species' persistence in a region are, then, its relation to other species and the presence of food, proper feeding zone, shelter from weather, and nesting sites (Andrewartha and Birch 1954, Grinnell 1914). In this section these factors as observed during the breeding season of the five species of warbler will be discussed.

The summer of 1956 was devoted to observations upon the four species, myrtle, black-throated green, blackburnian, and bay-breasted warblers, on their nesting grounds. The principal area studied was a 9.4 acre plot of mature white spruce (Picea glauca) on Bass Harbor Head, Mt. Desert Island, Hancock County, Maine. On 7 July 1956 the site of observations was changed to the town of Marlboro in Windham County, Vermont, where a red spruce (P. rubens) woodlot of comparable structure was studied. In the summer of 1957 more plots were studied. From 30 May until 5 June, eighteen plots of balsam fir (Abies balsamea), black spruce (P. mariana), and white spruce near Cross Lake, Long Lake, and Mud Lake in the vicinity of Guerette in Aroostook County, Maine, were studied. The remainder of the breeding season was spent on Mt. Desert Island, Maine, where five plots were censused. These will be described later.

Feeding Habits

Although food might be the factor for which birds compete, evidence presented later shows that differences in type of food between these closely related species result from differences in feeding behavior and position and that each species eats what food is obtainable within the characteristic feeding zone and by the characteristic manner of

feeding. For this reason, differences between the species' feeding positions and behavior have been observed in detail.

For the purpose of describing the birds' feeding zone, the number of seconds each observed bird spent in each of 16 zones was recorded. (In the summer of 1956 the seconds were counted by saying "thousand and one, thousand and two, . . ." all subsequent timing was done by stop watch. When the stop watch became available, an attempt was made to calibrate the counted seconds. It was found that each counted second was approximately 1.25 true seconds.) The zones varied with height and position on branch as shown in Figure 2. The height zones were ten foot units measured from the top of the tree. Each branch could be divided into three zones, one of bare or lichen-covered base (B), a middle zone of old needles (M), and a terminal zone of new (less than 1.5 years old) needles or buds (T). Thus a measurement in zone T3 was an observation between 20 and 30 feet from the top of the tree and in the terminal part of the branch. Since most of the trees were 50 to 60 feet tall, a rough idea of the height above the ground can also be obtained from the measurements.

There are certain difficulties concerning these measurements. Since the forest was very dense, certain types of behavior rendered birds invisible. This resulted in all species being observed slightly disproportionately in the open zones of the trees. To combat this difficulty each bird was observed for as long as possible so that a brief excursion into an open but not often-frequented zone would be compensated for by the remaining part of the observation. I believe there is no serious error in this respect. Furthermore, the comparative aspect is independent of this error. A different difficulty arises from measurements of time spent in each zone. The error due to counting should not affect results which are comparative in nature. If a bird sits very still or sings, it might spend a large amount of time in one zone without actually requiring that zone for feeding. To alleviate this trouble, a record of activity, when not feeding, was kept. Because of these difficulties, non-parametric statistics have been used throughout the analysis of the study to avoid any *a priori* assumptions about distributions. One difficulty is of a different nature; because of the density of the vegetation and the activity of the warblers a large number of hours of watching result in disappointingly few seconds of worthwhile observations.

The results of these observations are illustrated in Figures 2-6 in which the species' feeding zones are indicated on diagrammatic spruce trees. While

FIG. 2. Cape May warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

the base zone is always proximal to the trunk of the tree, as shown, the T zone surrounds the M, and is exterior to it but not always distal. For each species observed, the feeding zone is illustrated. The left side of each illustration is the percentage of the number of seconds of observations of the species in each zone. On the right hand side the percentage of the total number of times the species was observed in each zone is entered. The stippled area gives roughly the area in which the species is most likely to be found. More specifically, the zone with the highest percentage is stippled, then the zone with the second highest percentage, and so on until at least fifty percent of the observations or time lie within the stippled zone.

Early in the investigation it became apparent that there were differences between the species' feeding habits other than those of feeding zones. Subjectively, the black-throated green appeared "nervous," the bay-breasted slow and "deliberate." In an attempt to make these observations objective, the following measurements were taken on feeding birds. When a bird landed after a flight, a count

% OF TOTAL
NUMBER (4777)
OF SECONDS OF
OBSERVATION

% OF TOTAL
NUMBER (263)
OF
OBSERVATIONS

FIG. 3. Myrtle warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

% OF TOTAL
NUMBER (2611)
OF SECONDS OF
OBSERVATION
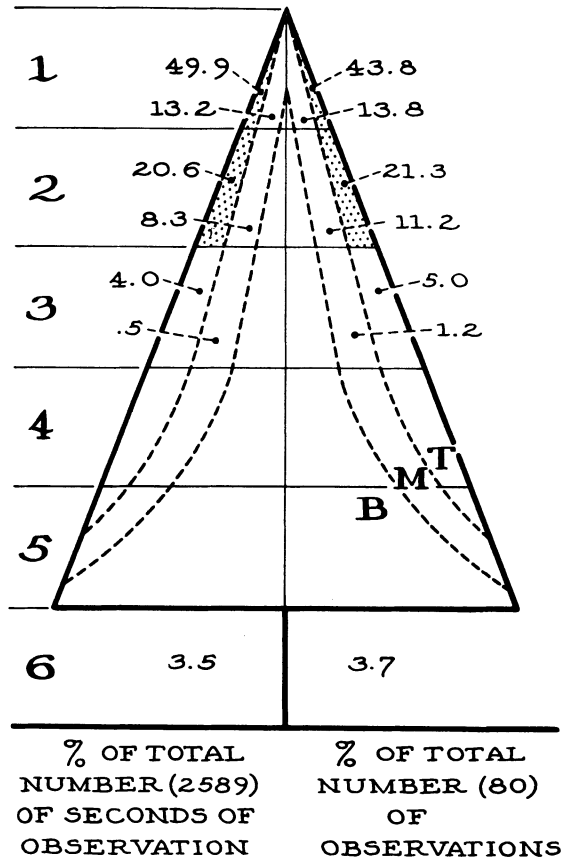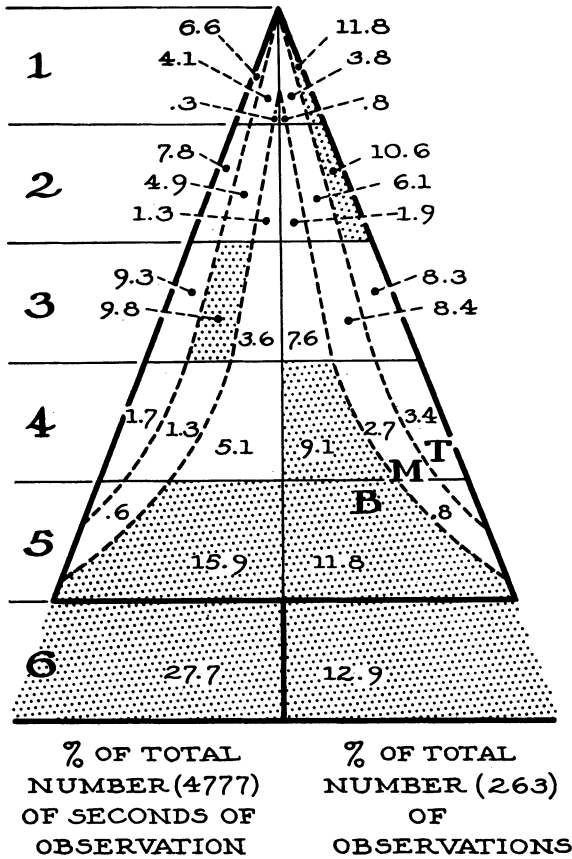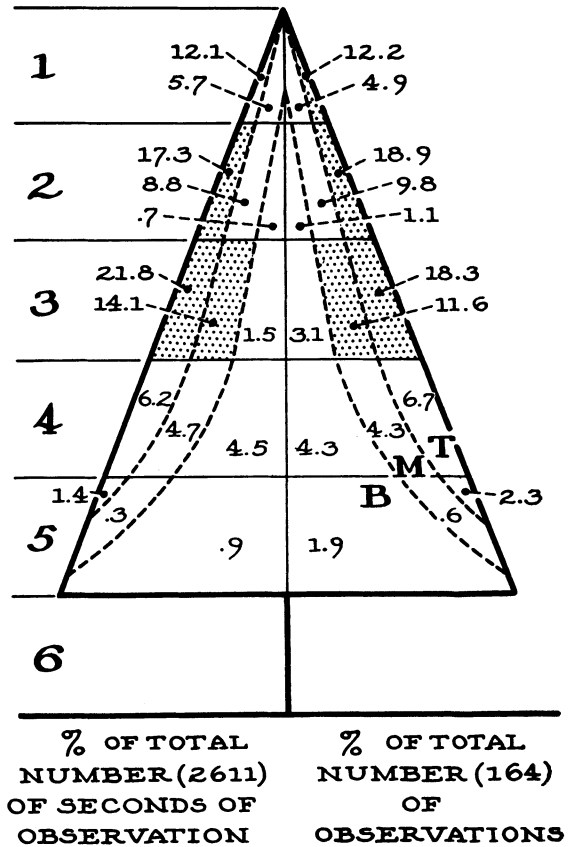
% OF TOTAL
NUMBER (164)
OF
OBSERVATIONS

FIG. 4. Black-throated green warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

of seconds was begun and continued until the bird was lost from sight. The total number of flights (visible uses of the wing) during this period was recorded so that the mean interval between uses of the wing could be computed.

The results for 1956 are shown in Table I. The results for 1957 are shown in Table II. Except for the Cape May fewer observations were taken than in 1956.

By means of the sign test (Wilson, 1952), treating each observation irrespective of the number of flights as a single estimate of mean interval between flights, a test of the difference in activity can be performed. These data are summarized in the following inequality, where $\dfrac{95}{<}$ is interpreted to mean "has smaller mean interval between flights, with 95% certainty."

their time searching in the foliage for food, some appear to crawl along branches and others to hop across branches. To measure this the following procedure was adopted. All motions of a bird from place to place in a tree were resolved into components in three independent directions. The natural directions to use were vertical, radial, and tangential. When an observation was made in which all the motion was visible, the number of feet the bird moved in each of the three directions was noted. A surpringing degree of diversity was discovered in this way as is shown in Figure 7. Here, making use of the fact that the sum of the three perpendicular distances from an interior point to the sides of an equilateral triangle is independent of the position of the point, the proportion of motion in each direction is recorded within a triangle. Thus the Cape May

$$\text{Black-throated green} \quad \underset{<}{95} \quad \left\{\begin{array}{l}\text{Blackburnian}\\\text{Myrtle}\end{array}\right\} \quad \underset{<}{99} \quad \left\{\begin{array}{l}\text{Cape May}\\\text{Bay-breasted}\end{array}\right\}$$

The differences in feeding behavior of the warblers can be studied in another way. For, while all the species spend a substantial part of

moves predominantly in a vertical direction, black-throated green and myrtle in a tangential direction, bay-breasted and blackburnian in a radial direc-

% OF TOTAL
NUMBER (1631)
OF SECONDS OF
OBSERVATION
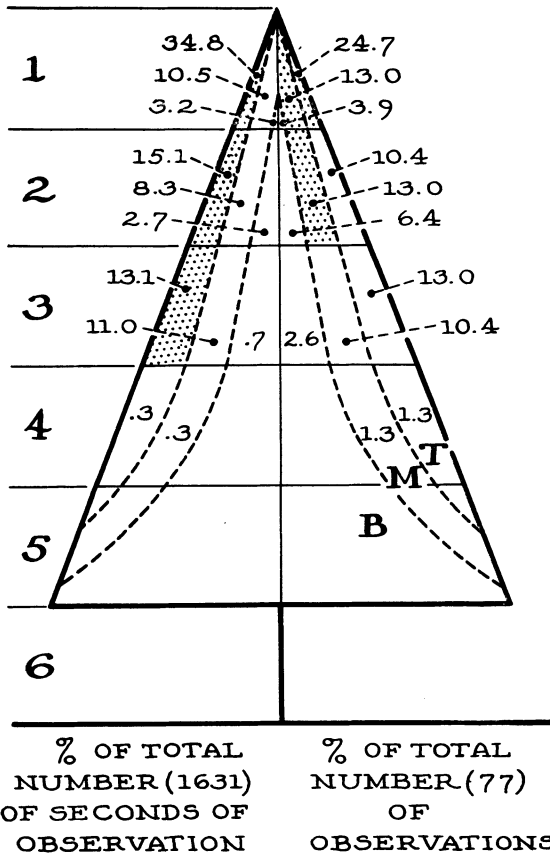
% OF TOTAL
NUMBER (77)
OF
OBSERVATIONS

FIG. 5. Blackburnian warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

% OF TOTAL
NUMBER (4166)
OF SECONDS OF
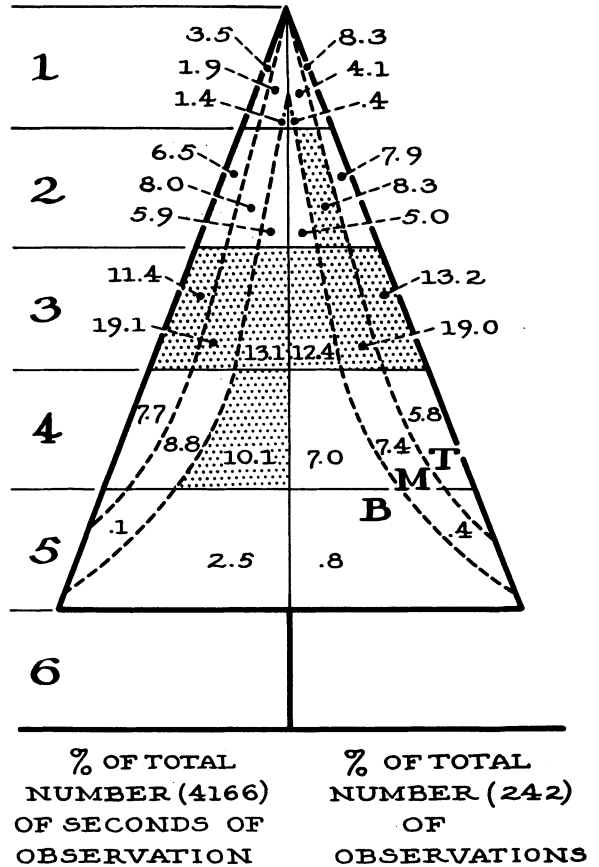OBSERVATION

% OF TOTAL
NUMBER (242)
OF
OBSERVATIONS

FIG. 6. Bay-breasted warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

tion. To give a nonparametric test of the significance of these differences Table III is required.

Each motion was classified according to the direction in which the bird moved farthest. Thus, in 47 bay-breasted warbler observations of this type, the bird moved predominantly in a radial direction 32 times. Applying a χ^2 test to these, bay-breasted and blackburnian are not different but all others are significantly (P<.01) different from one another and from bay-breasted and blackburnian.

There is one further quantitative comparison which can be made between species, providing additional evidence that during normal feeding behavior the species could become exposed to different types of food. During those observations of 1957 in which the bird was never lost from sight, occurrence of long flights, hawking, or hovering was recorded. A flight was called long if it went between different trees and was greater than an estimated 25 feet. Hawking is distinguished from hovering by the fact that in hawking a moving prey individual is sought in the air, while in hovering a nearly stationary prey indi-

vidual is sought amid the foliage. This information is summarized in Table IV.

Both Cape May and myrtle hawk and undertake long flights significantly more often than any of the other species. Black-throated green hovers significantly more often than the others.

At this point it is possible to summarize differences in the species' feeding behavior in the breeding season. Unfortunately, there are very few original descriptions in the literature for comparison. The widely known writings of William Brewster (Griscom 1938), Ora Knight (1908), and S. C. Kendeigh (1947) include the best observations that have been published. Based upon the observations reported by these authors, the other scattered published observations, and the observations made during this study, the following comparison of the species' feeding behavior seems warranted.

Cape May Warbler. The foregoing data show that this species feeds more consistently near the top of the tree than any species expect blackburnian, from which it differs principally in type

TABLE I. The number of intervals between flights (I) recorded in 1956 and the total number of seconds (S) of observation counted

	Myrtle		Black-throated green		Black-burnian		Bay-breasted	
	I	S	I	S	I	S	I	S
	1	40	4	45	1	5	5	55
	4	32	8	20	13	77	3	22
	4	13	6	60	2	11	2	33
	4	17	5	35	5	18	1	7
	2	10	5	23	5	24	3	37
	1	10	3	7	3	16	2	20
	5	25	9	35	3	18	1	7
	5	10	8	25	3	15	4	10
	5	11	1	12	4	11	11	60
	6	30	7	20	3	12	5	41
	3	10	7	39	4	46	3	50
	1	5	13	25	2	26	1	17
	13	68	5	10			1	3
	1	5	5	12			1	49
	1	7	2	37			4	42
	4	26					5	60
							5	35
							5	26
							3	14
							4	38
							3	14
							1	11
							3	22
							2	29
Total.........	60	319	88	405	48	279	78	702
Total Adjusted to True seconds	60	399	88	506	48	349	78	876

TABLE II. Intervals between flights and seconds of observation in 1957

	Cape May		Myrtle		Black-throated green		Black-burnian		Bay-breasted	
	I	S	I	S	I	S	I	S	I	S
	3	47	4	18	3	18	1	22	7	110
	12	35	1	62	5	22	3	22	2	115
	5	50	5	47	3	15	9	110	1	18
	2	15	3	17	13	89	7	26	1	22
	1	15	1	5	23	40	3	8	2	19
	1	45	12	86					2	47
	1	20							3	27
	4	29							8	112
	11	129							7	46
	6	47								
	1	15								
	4	50								
	3	20								
	21	122								
	1	12								
	·1	34								
	4	20								
	10	79								
Total...............	91	782	26	235	47	184	24	188	33	576
Adjusted 1956 Total...			60	399	88	506	48	349	78	876
Grand Total.........	91	782	86	644	125	690	72	537	111	1392
Mean Interval Between Flights.............		8.59		7.48		5.52		7.47		12.53

TABLE III. Number of times each species was observed to move predominantly in a particular direction. (Numbers ending in .5 result from ties)

Species	Radial	Tangential	Vertical	Total
Cape May.......	5.5	1.5	25	32
Myrtle..........	4.5	11.5	9	25
Black-throated green........	4	21	5	30
Blackburnian....	11	1	3	15
Bay-breasted....	32	7	8	47
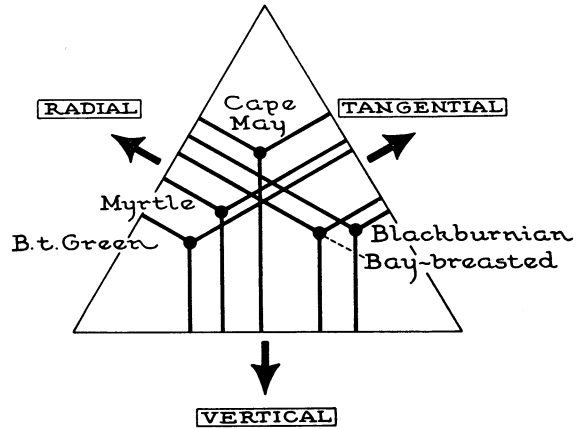
FIG. 7. Components of Motion. From the dot representing a species, lines are drawn to the sides of the triangle. The lengths of these lines are proportional to the total distance which the species moved in radial, tangential, and vertical directions, respectively.

TABLE IV. Classification of the flights observed for each species

Species	Long Flights	Hawking	Hovering	No. of Observ.
Cape May........	35	12	0	53
Myrtle...........	25	9	0	62
Black-throated green..........	1	0	7	42
Blackburnian......	0	1	0	35
Bay-breasted......	4	2	2	57

Applying χ^2 tests to pairs of species, the following conclusions emerge.

of feeding action. It not only hawks far more often than the blackburnian, but also moves vertically rather than radially in the tree, causing its feeding zone to be more restricted to the outer shell of the tree. Myrtle warblers when feeding in the tips of the trees nearly duplicate the feeding behavior of the Cape May. During rainy, windy, and cold weather Cape Mays were not found in the tree tops, but were instead foraging in the low willows (*Salix* sp.) and pin cherries (*Prunus pensylvanica*). Here they often fed among the flowers, for which their semitubular tongue (Gardner 1925) may be advantageous.

Because of this species' irregular breeding dis-

tribution, both in space and time, and its former rarity, there are very few published descriptions of its feeding behavior. Knight (1908), although he lived in Maine, had never seen one. Brewster (Griscom 1938) wrote that:

"It keeps invariably near the tops of the highest trees whence it occasionally darts out after passing insects. . . . In rainy or dark weather they came in numbers from the woods to feed among the thickets of low firs and spruces in the pastures. Here they spent much of their time hanging head downward at the extremity of the branches, often continuing in this position for nearly a minute at a time. They seemed to be picking minute insects from under the surface of the fir needles. They also resorted to a thicket of blossoming plum trees directly under the window, where we were always sure of finding several of them."

He also said that it was more active than the bay-breasted. Bond (1937) stated that all feeding was done more than twenty feet above the ground. Kendeigh (1947) said males tend to sing about seven feet from the tops of the trees, and that feeding is done at the same level. He also mentions that the birds sometimes hawk after passing insects. The rainy weather observations indicate behavior very much like that of winter and migration to be discussed later.

Myrtle Warbler. This species seems to have the most varied feeding habits of any species. Although it moves slightly more in a tangential direction than any except black-throated green, it is probably more correct to think of the myrtle as having the most nearly equal components (radial, tangential, and vertical) of any species. This is shown by its most nearly central location in Figure 7. It is also seen to have the most widely distributed feeding zone, although the ground feeding was nearly, but not completely, restricted to the gathering of emerging Tipulids for newly hatched young. Sometimes a substantial amount of this is hawking for flying insects; at other times it is largely by rapid peering (Grinnell 1921) amid the thick foliage near the tree tops. Myrtle, along with Cape May, makes a much higher proportion of flights to other trees than do the other species, often flying from one side of its territory to the other with no apparent provocation. The other three species tend to search one tree rather thoroughly before moving on. Further evidence of the plasticity of the myrtle warbler's feeding habits will be presented when the other seasons are considered. Grinnell and Storer (1924) stated that the Audubon's warbler (which often hybridizes with the myrtle and with it froms a superspecies (Mayr 1950)) also feeds in peripheral foliage and does a greater amount of hawking than other species. Kendeigh (1947) said that

birds fed from ground to tops of trees, and also that two males covered two and four acres respectively in only a few minutes. Knight (1908) said "Many of the adult insects are taken on the wing, the warblers taking short springs and flights into the air for this purpose. The young for the first few days are fed on the softer sorts of insects secured by the parents, and later their fare is like that of the parents in every way."

Black-throated Green Warbler. Compared to the myrtle warbler this species is quite restricted in feeding habits. As seen in Figure 4, it tends to frequent the dense parts of the branches and the new buds, especially at mid elevations in the tree. Most of its motion is in a tangential direction, keeping the bird in foliage of a nearly constant type. It has the shortest interval between flights of any of the five species and thus appears the most active. Almost all feeding seems to be by the method of rapid peering, necessitating the frequent use of the wings which the observations indicate. The foliage on a white spruce is a thick, dense mat at the end of the branch, changing to bare branch rather more sharply than in the red spruce. The black-throated greens characteristically hop about very actively upon these mats, often, like the other species, looking down among the needles, and just as often, unlike the myrtle and bay-breasted, peering up into the next mat of foliage above. When food is located above, the bird springs into the air and hovers under the branch with its bill at the point whence the food is being extracted. While other species occasionally feed in this fashion, it is typical only of the black-throated green. After searching one branch, the black-throated green generally flies tangentially to an adjacent branch in the same tree or a neighboring one and continues the search. Only rarely, during feeding, does it make long flights. While it occasionally hawks for flying insects (missing a substantial proportion), this is not a typical behavior and the birds seldom sit motionless watching for flying insects in true hawking behavior. During its feeding, this species is very noisy, chipping almost incessantly, and, if it is a male and if it is early in the season, singing frequently. The other species are very quiet. A portion of this behavior can be confirmed from the literature. Knight (1908) said "Only rarely do they take their prey in the air, preferring to diligently seek it out among the branches and foliage" and Stanwood (Bent 1953) said "The bird is quick in its movements, but often spends periods of some length on one tree." Like the myrtle, this species enlarges its feeding zone while gathering food for its young. This is similar to the results of Betts (1955)

indicating that the young tits eat different food from the adults.

Blackburnian Warbler. This species generally feeds high in the trees but is otherwise more or less intermediate between black-throated green and bay-breasted in its feeding behavior. This is true both of its flight frequency and its preferred feeding position on the limb (Figure 5). It is also intermediate in its method of hunting, usually moving out from the base to the tip of the branches looking down in the fashion of the bay-breasted and occasionally hopping about rapidly upon the mat of foliage at the branch tips looking both up and down for insects and even hovering occasionally. They seem to use the method of rapid peering, only occasionally hawking after a flying insect. As further evidence, Knight (1908) wrote "As a rule they feed by passing from limb to limb and examining the foliage and limbs of trees, more seldom catching anything in the air." Kendeigh (1945) said "It belongs to the treetops, singing and feeding at heights of 35 to 75 feet from the ground."

Bay-breasted Warbler. The usual feeding habits of this species are the most restricted of any of the species studied. All of the observations in the T1 zone and most in the T2 zone refer to singing males. This species uses its wings considerably less often than the other species, although it still appears to use the method of rapid peering in its hunting since it moves nearly continuously. These motions are, however, predominantly radial and seldom require the use of wings. The bird regularly works from the licheny base of the branches well out to the tip, although the largest part of the time is spent in the shady interior of the tree. It frequently stays in the same tree for long periods of time. This species very rarely hovers in the black-throated green fashion, and appears much less nimble in its actions about the tips of the branches, usually staying away from those buds which are at the edge of the mat of foliage. When it does feed at the edge of the mat, it is nearly always by hanging down rather than peering up. Other observers have emphasized the slowness. Brewster (Griscom 1938) called this warbler "slow and sluggish," and Kendeigh (1947) said "The birds do not move around much, but may sing and feed for long periods in the same tree." Forbush (1929) stated that it spends most of its time "moving about deliberately, after the manner of vireos."

Food

Two species may eat different food for only three reasons: 1. They may feed in different places

or different times of day; 2. They may feed in such a manner as to find different foods; 3. They may accept different kinds of food from among those to which they are exposed. (Of course, a combination of these reasons is also possible.)

In the previous section it was shown that the warblers feed in different places and in a different manner, thus probably being exposed to different foods for the first and second reasons mentioned above. It is the aim of this section to show that the five warbler species have only small differences of the third kind. Theoretically, such differences, unaccompanied by morphological adaptations, would be disadvantageous, for, lacking the adaptations required to give greater efficiency in food collecting, and suffering a reduction in the number of acceptable food species, a bird would obtain food at a lesser rate. When the necessary adaptations are present, they usually consist of quite marked differences in bill structure such as those reported by Huxley (1942), Lack (1947), and Amadon (1950). As Table V shows, the mean bill measurements in millimeters of the five species of warbler considered in this study are quite similar. Twelve specimens of each species from the Peabody Museum of Natural History at Yale University were measured for each of the means given.

TABLE V. Mean dimensions of the bills of 12 specimens of each species

Species	Bill Length	Height at Nares	Width at Nares	Width 2.5mm from tip
Cape May	12.82	2.85	2.93	0.96
Myrtle	12.47	3.26	2.12	1.33
Black-throated green	12.58	3.38	3.15	1.34
Blackburnian	12.97	3.24	3.36	1.17
Bay-breasted	13.04	3.69	3.58	1.43

The Cape May alone has a noticeably different bill, it being more slender, especially at the tip. This bill houses a semi-tubular tongue as mentioned above, which is unique in the genus. These may be useful adaptations for their rainy weather flower feeding, but would seem ill-adapted for the characteristic flycatching of the breeding season (Gardner 1925). It is doubtless useful in other seasons, as will be discussed later. Aside from the Cape May, all other species differ in bill measurement by only a small fraction of a millimeter. Thus, for theoretical reasons, no pronounced differences of the third kind would be expected. Empirically, there is evidence to support this belief.

McAtee (1932) reported upon the analysis of eighty thousand bird stomachs, in an effort to

disprove mimicry. Although his results were not conclusive, he claimed that insects appeared in bird stomachs about proportionately to their availability. Kendeigh (1945) agreed with this conclusion. Although McAtee (1926) said that no detailed studies of warbler food habits had been made, and no general ones seem to have appeared since, two very suggestive sets of analyses covering the five species have been published. Kendeigh (1947) reported upon the stomach contents of a collection made near Lake Nipigon, and Mitchell (1952) analyzed the stomachs of many birds taken during a budworm infestation in Maine. These data show, first, that most species of warbler eat all major orders of local arboreal arthropods. Furthermore, although there are differences in proportion of types of foods eaten by various species, these differences are most easily explained in terms of feeding zone. Thus, black-throated green and blackburnian which are morphologically the most similar of the five species have quite different foods. Kendeigh's table shows that black-throated green eats 4% Coleoptera, 31% Araneida, and 20% Homoptera, which blackburnian eats 22% Coleoptera, 2% Araneida, and 3% Homoptera. Dr. W. R. Henson has pointed out (pers. comm.) that Coleoptera can reasonably be assumed to come from inner parts of the tree where blackburnian has been shown to feed, whereas the Homoptera and most of the Araneida would be caught in the current year's growth where the black-throated green feeds more often, thus explaining the observed difference. Black-throated green and bay-breasted, with the most vireo-like bills (high at the nares), seem to eat more Lepidoptera larvae which are typical vireo food, but Mitchell's table shows that the other species too can eat predominantly Lepidoptera larvae when these are abundant. Otherwise, the food of the bay-breasted is more like that of the blackburnian, the feeding habits of which are similar. There are not sufficient data to analyze Cape May in this fashion. The myrtle warbler's feeding behavior is so flexible that no correlation between insects caught and a specific feeding zone or behavior is expected. This is shown by its having the most even distribution of food of any of the species considered. Thus, these correlations show that the differences in warbler food can be readily explained by morphological and zonal characteristics of the species.

Nest Location

The position of the nest is quite characteristic in warbler species. Nearly all species of the genus *Dendroica* nest off the ground. Figure 8 shows

heights of the nests of the five species of warbler studied here. These data result from a combination of the records of Cruickshank (1956), the information in the egg collection of the American Museum of Natural History in New York, and that gathered in this study. Since the distributions are skewed and irregular, the median and confidence intervals for the median (Banerjee and Nair 1940) are appropriate measurements. As the figure shows, the Cape May, with 95% confidence interval for the median of 40-50 feet, and the blackburnian, whose interval is 30-50 feet, have quite similar nest heights, probably reflecting their tendency to feed at high elevations. The Cape May's nest is virtually always near the trunk in the uppermost dense cluster of branches in a spruce or occasionally a fir. The blackburnian may nest in a similar location or may nest farther out toward the branch tips. Myrtle and black-throated green have similar nesting heights, both species having 95% confidence interval for the median nest height of 15-20 feet. The black-throated green seems to prefer smaller trees for its nest, and is thus more likely to place its nest near the runk, but, in keeping with its other characteristics, the myrtle seems quite varied in this respect. Finally, the bay-breasted, which has the lowest feeding zone, has the lowest nest position, the median height being between 10 and 15 feet (95% confidence). Thus, the nest positions of the five species of warbler reflect their preferred feeding zones.

Territoriality

Defining territory as any defended area, warbler territories in the breeding season are of what Hinde (1956) called type A ("Large breeding area within which nesting, courtship, and mating and most food-seeking usually occur"). He pointed out that, since the behavioral mechanisms involved in defending a territory against others of the same species are the same as those involved in defending it against other species, this distinction need not be specified in the definition. From the ecological point of view, the distinction is of very great importance, however, for, as G. E. Hutchinson pointed out in conversation, if each species has its density (even locally) limited by a territorial behavior which ignores the other species, then there need be no further differences between the species to permit them to persist together. A weaker form of the same process, in which territories were compressible but only under pressure of a large population, would still be effective, along with small niche differences, in making each species inhibit its own population growth more than the others'—the
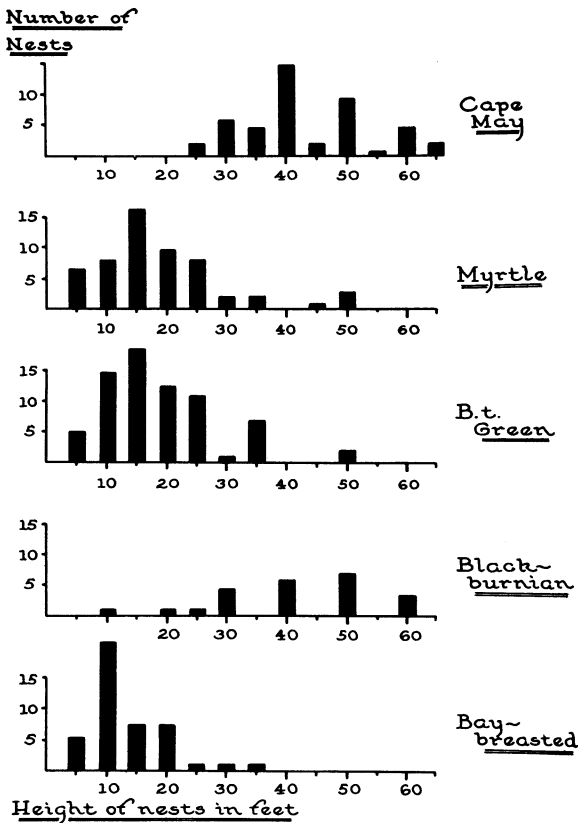
Fig. 8. Nesting heights of warblers.

necessary condition for the persistence of sympatric species.

Two further conditions make territory important for regulating populations. First, to have density dependent regulation, a species' regulating mechanism must have information of its own population density. Second, a predator ideally should keep its prey at that population level which permits the greatest rate of production. This means that the prey would not normally be particularly scarce. This, combined with the varied prey of the birds and the varied predators of the insects, would make food density a poorer criterion of a given bird species' density than size of territory. Thus, competition for food would be reduced from a "scramble" to a "contest" (Haldane 1955).

While the true nature of birds' territories has proved very elusive (Lack 1954, Hinde 1956), two separate lines of evidence suggest strongly that territories contribute to the regulation of local densities in warbler populations. Stewart and Aldrich (1951) and Hensley and Cope (1951) removed adult birds from their territories in 1949 and 1950 respectively, in a 40 acre plot in a budworm-infested area of Maine. The vacated territories were always filled by new pairs, the males

singing the vigorous song of a bird setting up a territory. It seems nearly inescapable that these were part of a large floating population of birds only prevented from breeding by the absence of unoccupied territories. Since this was in a budworm outbreak, there seems little doubt that there would have been adequate food for a larger breeding population.

In a study over a series of years on the birds in New Brunswick, Cheshire (1954) recorded the populations and territory sizes of the various species as a budworm outbreak began and progressed. He showed that while the bay-breasted warbler (the commonest bird during the outbreak) underwent a five- to seven-fold increase as the outbreak began, their mean territory sizes remained constant instead of decreasing correspondingly. That is, there had been unoccupied interstices between territories initially; these were filled in by the incoming birds but territory sizes were left unchanged.

The facts suggest that the territory size is more or less fixed in this region (although, of course, it may vary from region to region) and that if territorial compression occurs during high population densities, it only does so during higher population densities than those observed. Of course, if high population densities persisted, natural selection might be expected to reduce territory size, but this is a different situation.

As for interspecific territoriality, there is no exclusion of the kind found in intraspecific territoriality, as is clearly shown in Kendeigh's (1947) territory maps. It is very difficult to distinguish a mild repulsion of other species by territorialism from a preference for slightly different habitats. Adequate information does not exist to make the distinction at present. However, it seems quite certain that interspecific territoriality is weaker than intraspecific and, therefore, that the effect of a large density of one species is greater on that species than on the others. It is thus probable that, in the warblers, territoriality helps reduce competition and acts as a stabilizing factor (as well as performing the well-known functions of pair formation and maintenance).

Natality and Mortality

In a population which has reached an equilibrium size, abundance is independent of birth and death rates. For species in equilibrium, then, a study of birth and death rates is not necessary to understand the control of the equilibrium abundance. However, as Darwin (1859) said, "A large number of eggs is of some importance to those species which depend upon a fluctuating

amount of food, for it allows them rapidly to increase in numbers."

The five species of warbler studied here are very interesting in this respect. Table VI is a summary of the nesting data of the Museum of Comparative Zoology at Harvard, the American Museum of Natural History in New York, and the data of Harlow published by Street (1956).

TABLE VI. Mean clutch sizes for the 5 species

Species	No. of Nests	CLUTCH SIZE					Mean	St. Dev.
		3	4	5	6	7		
Cape May........	48		4	11	24	9	5.792	.850
Myrtle............	24	1	19	4			4.125	.449
Black-throated green.........	45	2	39	4			4.044	.366
Blackburnian......	44	7	32	5			3.955	.526
Bay-breasted......	49			5	21	20	3	5.429	.752

Cape May and bay-breasted warblers' nests were enough of a prize that it is quite certain that all found were kept and that the collections do not reflect any bias. There is a possibility of slight bias, collectors perhaps prizing larger clutches, in the other three species in the museum collections, but their clutch sizes are so constant that this seems improbable. The data of Harlow are not subject to his criticism, since he recorded all nests found.

While the sources of these collections vary in latitude from that of the Poconos of Pennsylvania to that of northern New Brunswick, there appears to be very little change in clutch size in this range of latitude. Thus the mean clutch size of 16 nests of the black-throated green in the Poconos is 4.06, while for the combined collections from Nova Scotia and New Brunswick (12 nests) the mean clutch is 4.17. The nests of the other species are from a narrow range of latitude and would not be expected to vary. Thus it was felt permissible to combine the data from different latitudes.

It is immediately apparent that Cape May and bay-breasted, the species which capitalize upon the periodic spruce budworm outbreaks, have considerably larger clutches than the other species, as Darwin would have predicted. It is of interest that the only other warbler regularly laying such large clutches is the Tennessee warbler (*Vermivora peregrina*) which is the other species regularly fluctuating with the budworms (Kendeigh 1947). Thus it seems that Darwin's statement provides an appropriate explanation for the larger clutches. It is also interesting that the standard deviation of the Cape May and bay-breasted warblers' clutch sizes is greater. This suggests a certain plasticity which can be verified, for the

bay-breasted at least, as follows. If the time of the budworm outbreak in New Brunswick is taken as 1911-1920 (Swaine and and Craighead 1924), and other years from 1903 until 1938 are called non-budworm years, the bay-breasted warbler clutches from northeastern New Brunswick can be summarized as follows:

	Clutch Size			
	4	5	6	7
Budworm Years	1	5	15	3
Non-budworm Years	4	8	5	0

The U test (Hoel 1954) shows this to be significant at the .0024 level; that is, bay-breasted warblers lay significantly larger clutches during years of budworm outbreaks. There are not sufficient data to make a corresponding comparison for Cape May warblers. It is known (Wangersky and Cunningham 1956) that an increase in birth rate is likely to lead to instability. The easiest way to increase the stability, while still maintaining the large clutch which is desirable for the fluctuating food supply, is to have the clutch especially large when food is abundant. This is apparently the solution which the bay-breasted warbler, at least, has taken.

Mortality during the breeding season is more difficult to analyze. Disease is not normally important as a mortality factor in passerines (Lack, 1954) and this appeared to be the case for the warblers under observation. Predation may be important, however. Saw-whet owls (*Aegolius acadica*), Cooper's hawks (*Accipiter cooperii*), goshawks (*A. gentilis*), ravens (*Corvus corax*), crows (*C. brachyrhynchos*), and herring gulls (*Larus argentatus*) all occasionally were noted in the Maine woods, but no evidence was obtained of their preying upon the warblers. In fact, none of the established pairs of birds were broken up by predation of this type. Red squirrels (*Tamiasciurus hudsonicus*) were continually present in all plots and were frequently observed searching for nests. They certainly destroyed the nest of a black-throated green and of a brown creeper (*Certhia familiaris*) and were quite probably responsible for plundering one myrtle warbler nest which was robbed soon after eggs were laid. The most common evidence of mortality, however, was the frequent observation of parents feeding only one or two newly fledged young. Thus two pairs of myrtle warblers in 1956 and one in 1957 were observed the day the young left the nest feeding four young. One of the 1956 pairs succeeded in keeping all four young alive for at least three days, at which time they could no longer be fol-

lowed. The remaining two pairs were only feeding two young on the day following the departure of the young from the nest. Similarly, of two black-throated green pairs (one in 1956, one in 1957) where young could be followed, one kept all four young alive and the second only raised two of the fledged four. It was difficult to determine the number of young the parents were feeding. It was also difficult to be at the nest site when the young left the nest to determine the number of fledged young. Consequently, no more observations suitable to report were made. When the young leave the nest, they fly to nearby trees quite independently of one another and apparently never return to the nest. The result is that within a few hours the young are widely scattered. In this condition they are very susceptible to predators and exposure, and should one fly when its parents were not nearby, it would rapidly starve. Normally, the young only fly or chatter loudly when a parent with food is calling nearby, and the parents seem remarkably good at remembering where the young have gone. At best, however, this is a very dangerous period. It is of some interest to note that adult warblers will feed not only young of other birds of their own species but also of other species. Skutch (1954) reviewed several published cases of this. Hence, when a wood is densely settled with warblers, the members of a large clutch might have a better chance of surviving, the straying young being fed by neighbors. This high density is, of course, the situation which obtains during a budworm outbreak when bay-breasted and Cape May warblers are so successful.

Time of Activities

So far, the nature and position of the species' activities during the breeding season have been compared. The time of these activities would also be a potential source of diversity. There could either be differences in the time of day in which feeding took place, or there could be differences in the dates during which eggs were laid and the young fed. The first type of difference (time of day) seems inherently improbable since, at least while feeding the fledged young, the parents are kept busy throughout the daylight hours gathering food. Record was taken of the time at which the various warbler species began singing in the morning of 19 June 1956. The results (Eastern Daylight Time) are: 0352, first warbler (magnolia, *D. magnolia*); 0357, first myrtle; 0400, both myrtle and magnolia singing regularly; 0401, first black-throated green; 0402, first parula warbler (*Parula americana*); 0403, first bay-breasted;

0405, all warblers singing regularly. Thus, within 13 minutes after the first warbler sang all species were singing regularly. The sequence of rising corresponds to the degree of exposure of the usual feeding zones for that date (see Figures 2-6), and therefore probably depends only upon the time at which the light reaches a certain intensity.

As for the breeding season, there is good evidence of differences in time of completion of clutches. Since date of completion can be expected to change from place to place, comparisons must be made at one fixed locality. Of 15 nests of black-throated green warbler found by Harlow in the Poconos of Pennsylvania, the mean date of clutch completion was June 3, and of 21 blackburnian the mean date of clutch completion was June 1. Thus, for this region, and there is no reason to think that the relative dates are different in other regions, there is little difference in time of nesting between blackburnian and black-throated green warblers. From the extensive collections of P. B. Philipp near Tabusintac, N. B., now in the American Museum of Natural History, and from a smaller number collected in the same region by R. C. Harlow, now in the Museum of Comparative Zoology, bay-breasted and Cape May warbler nest dates can be compared (Figure 9). It is quite clear that the bay-breasted with the median date of nest discovery of 25 June (95% confidence interval for the median 23-27 June) nest substantially later than the Cape May whose median date is 17 June (95% confidence interval for the median of 16 June-20 June). As the figure shows, the small number of nests of black-throated green and myrtle from the same region show a fairly wide spread but strongly suggest median dates intermediate between Cape May and bay-breasted. (The dates recorded by Palmer (1949) for Maine give a roughly similar sequence; myrtle, 30 May-6 June; black-throated green, 26 May-20 June; bay-breasted, after 7 June.)

It might be expected that the insects caught by the species which feed in the T zones and near the tree tops would reach peak abundance sooner thus making it desirable for those species to nest earlier. The sequence of nesting dates just presented seems to be consistent with this hypothesis.

EVIDENCE FROM WINTER SEASON

The five species of warbler migrate out of the coniferous forest through the deciduous forest and cultivated land in eastern North America and, mostly, into the West Indies and Central and South America. Therefore, any behavioral char-

FIG. 9. Nesting dates of warblers in the Tabusintac, N. B., region.

acteristics that remain the same throughout the year must be nearly independent of the specific environment (at least within the range of environmental variation to which the bird is normally exposed). If any aspects of the breeding season behavior are retained throughout the year, these would be expected to be more fundamental than those aspects that varied with the local environment. This would be especially likely if the retained aspects of the behavior were controlled by morphological characteristics. The varying aspects would be interpreted as the result of interaction between the fundamental characteristics and the environment, as direct results of stimuli particular to that environment, or as seasonal aspects of birds' physiology. Thus it is of interest to compare behavior in different seasons.

Winter Distribution

Although Salomonsen (1954) said that species which breed in the same place tend to winter in different geographic regions, there is no evidence for this in the five warblers. More precisely, Salomonsen's statement suggests that a certain amount of competition might be avoided by having allopatric wintering grounds. Probably the most satisfactory way to test this is to determine whether the five warblers' ranges show less winter overlap than a randomly chosen group of five eastern warblers (Western warblers tend to winter in a different region and hence should not be included). To make definitions precise, two species of warbler were said to have a significant overlap in winter ranges if at least half of one species' winter range is included in the other's. From the winter range data of Bent (1953) the twenty-three species of warbler breeding in Maine (Palmer, 1949) show 253 significant overlaps,

i.e., an average of 11 per species. Therefore, the probability that a randomly chosen pair of species of Maine warblers will show significant winter range overlap is 11/23 or .478. Considering the five species of warbler in the present study, Cape May overlaps with myrtle and possibly black-throated green; myrtle overlaps with Cape May, black-throated green, and blackburnian; black-throated green overlaps with Cape May (possibly), myrtle, and blackburnian; blackburnian overlaps with myrtle, black-throated green, and bay-breasted; and bay-breasted overlaps with blackburnian. There is thus a total of 10 certain overlaps among the 5 species, or 2 per species. There is thus a mean overlap per pair of species of 2/5 or .400 which is quite near the expected 0.478 suggesting that the five species overlap about randomly. It might be argued that the 23 species of Maine warblers themselves show a mutual repulsion in the winter ranges and hence are a poor standard of comparison. That this is not so can be seen as follows. The 23 species have a total of 315 significant summer overlaps in range, or 13.7 per species; i.e., 13.7/23 or 0.596 is the probability that a randomly chosen pair of species will overlap in summer. As discussed above, the probability is 0.478 that a randomly chosen pair will overlap in winter. Therefore, if winter range is chosen independently of summer, 0.478 x 0.596 = 0.285 would be the expected probability of significant overlap in both winter and summer. Significant summer and winter overlaps were recorded in 164 cases, giving 7.1 per species, or a probability of 7.1/23 = 0.309, which is even a very slightly higher figure than expected, showing a slight tendency for birds which summer together to winter together. Therefore, the Maine warblers do not repel one another in over-all winter range and they are therefore suitable for the comparison made earlier. It can be concluded that the five species show about the amount of overlapping of winter range that would be expected on a random basis.

This does not prove that the species occupy the same habitat in the winter, of course. Although there are no adequate data to investigate the problem, it is quite possible that because of habitat selection, wintering populations of the five species are isolated.

Winter Feeding Behavior

The period of 22 December 1956 until 9 January 1957 was spent in Costa Rica observing winter behavior of warblers. Although myrtle, black-throated green, and blackburnian warblers include Costa Rica in their winter range (Skutch,

in Bent 1953, and pers. comm.), only black-throated green of the five were found during the author's study. However, many other species of warbler were present, and detailed notes were taken on them for comparison with summer behavior. Measurements of interval between flights were made for each species. These should be comparable with those made in other seasons. No strictly comparable measurement of feeding position could be made, however. In view of the great variety of tree heights in tropical forests, measurements of feeding height could not reasonably be made in terms of distance from the top of the tree. Instead, height above the ground was used, usually gauged by eye and occasionally checked by camera viewfinder. Zones such as base, middle, and tip of branch were not reasonable, but general reference to large limbs or leaves could be made. The actual behavior while gathering food is probably comparable with other seasons; it is fairly subjective, however, so that the comparison should be confirmed by the various other measurements. A general comparison of winter and summer behavior of warblers wintering in Costa Rica will be given first; this will be followed by a more detailed analysis of two species.

Thirteen species of Parulidae were observed in Costa Rica. Of these, nine, black and white (*Mniotilta varia*), Tennessee, golden-winged (*Vermivora chrysoptera*), yellow, black-throated green, sycamore (*Dendroica dominica albilora*)[2], chestnut-sided (*Dendroica pensylvanica*), Wilson's (*Wilsonia pusilla*), and redstart (*Setophaga ruticilla*), breed in northeastern United States and/or adjacent Canada. Their summer behavior has been observed, somewhat casually, by ornithologists for many years. These observations are summarized in a general way by Bent (1953) and are part of the common knowledge of most ornithologists. It is therefore of great interest that Skutch, who has made very careful observations of Central American birds, has stated (pers. comm.) that he thinks all warblers wintering in Costa Rica (except perhaps chestnut-sided which he feels spends more time in high trees in the winter) have the same general feeding behavior and feeding height in both seasons. Table VII summarizes general results of this study and helps confirm Skutch's impression.

Tennessee and black-throated green were observed in greater numbers than the others. Hence, a detailed comparison of their winter behavior in relation to their summer behavior is possible. Tennessee warblers often hopped along branches, while black-throated green more often hopped

[2] Rare in Costa Rica.

TABLE VII. Summary of observations in Costa Rica

Species	COSTA RICA			BREEDING GROUNDS	
	Approx. Number Observed	Principal Feeding Height	Principal Feeding Activities	Principal Feeding Height	Principal Feeding Activities
Black and White....	5	0-35'	creeps on trunk and branches	same	same
Golden-winged......	1	5-25'	hops	same	same
Tennessee.........	200	10-50'*	hops, esp. along branches*	0-40'	same*
Yellow...........	20	4-40'	hops	same	same
Black-th. green.....	50	10-50'*	hops, esp. across branches*	same*	same*
Sycamore.........	1	8-30'	creeps and hops	?	same
Chestnut-sided......	15	0-50'	hops	0-30'	same
Wilson's..........	15	0-25'	hops	same	same
Amer. redstart......	10	5-50'	hawks for flying insects	same	same

*See text for further information.

across branches. To measure this tendency, the following procedure was adopted. A count was made of the number of changes of feeding branch which required hopping or flying over a gap. The number of seconds of observation was also recorded. If Tennessees moved along branches, they should have had significantly fewer hops per second than black-throated greens which moved across branches. In the table below H stands for the number of hops or flights across an air gap in S seconds.

Black-throated green		Tennessee	
H	S	H	S
		4	30
8	90	3	48
5	38	6	105
7	43	4	54
1	14	6	100
12	85	11	74
12	60	8	83
14	70	8	82
59	400	50	576

Mean No. of
Seconds per
hop   6.78   11.52

Black-throated greens thus hopped 59 times in 400 seconds for a mean number of seconds per hop of 6.78. Tennessees hopped 50 times in 576 seconds for a mean number of seconds per hop of 11.52. By an extended sign test (Dixon and Massey 1951) this difference is well within the 5.5% level of significance. Hence, it is clear that black-throated greens hop across branches more

often than Tennessees, partially confirming the subjective impression described above.

Strictly comparable measurements cannot be made in the breeding season since black-throated green feeds in coniferous and Tennessee in deciduous trees. However, the black-throated green has been shown to move principally in a tangential direction in the summer, while of eleven Tennessee warbler observations in the summer of 1957 all showed the hopping along branches which characterized the winter feeding behavior.

From these data, it is evident that the general aspects of warbler behavior are nearly the same in winter and summer. For warblers wintering in the West Indies the same situation obtains; namely, the winter habitats bear no obvious similarity to those chosen in the breeding season, but the feeding behavior and height are roughly the same (Eaton 1953). Cape May and myrtle warblers are particularly interesting and a little atypical in this respect. Both Bond (1957) and Eaton mention that Cape May frequents gardens and plantations, where it is often near the ground. This behavior parallels that observed by Brewster in the summer and reported earlier. In the winter it spends much of its time feeding upon flowers, a fact which will be used later. Bond (1957) and Skutch (in Bent 1953) both mention that myrtle warblers, in their West Indian and Central American wintering grounds, are found from beaches to forests, frequenting open ground especially. This variety of feeding location combined with its enormous winter range confirms the summer observation of great flexibility of behavior.

These observations on the flexibility of myrtle warblers can be extended by including observations made on their wintering grounds in the United States. It is well known (Pettingill 1951) that myrtles winter in the northeast wherever there are extensive patches of bayberry (*Myrica pensylvanica*). Montauk Point on Long Island, which is such a place, was visited on January 26, 1957. Here myrtles were the commonest bird in the habitat in which the bayberry is abundant. The myrtles were moving about in flocks, frequently, as in the summer, making long flights. They fed principally while hopping upon the fallen leaves under bayberries. (There was no snow.) This behavior was very similar to that observed in the summer while they were catching emerging crane flies. Some were feeding upon the "wax" coat of the berries which is readily digestible and contains nodules which are rich sources of proteins and carbohydrates (Hausman 1927).

POPULATION CONTROL

Any factor that can control a local population has a space distribution. Examples of such factors are food, nesting sites, and predators. Thus all populations are limited by the amount of suitable space. The meaning of "suitable" for a given species is the interesting problem. Within a given environment each necessary activity requires a certain amount of space. That activity which requires the greatest amount of space is likely to be limiting. Thus, animals such as barnacles which wait for moving food to pass by and require very little space to catch it are likely to be limited by amount of surface on which to rest. Here "suitable space" means "space adequate for barnacle attachment." Similarly, for some insects the suitable space may be the space with sufficient food supply within easy dispersal distance; for some birds, suitable nest holes may be scarcer than adequate food and suitable space will mean proper nest hole. This section will be devoted to the nature of suitable space for the five species of warbler under consideration.

The five warblers do not seem to have special nesting space or nesting material requirements which would necessitate a larger amount of space than food gathering. Territory defence is probably the only activity of the warblers that requires an area of comparable size to that needed for food gathering. As discussed earlier, territoriality may exert a limiting effect upon populations under conditions of abundant food supply, thus acting as a stabilizing factor. However, if territory requirements limit populations under normal conditions, it may be inquired why natural selection has not reduced territory sizes thus permitting larger populations. Furthermore, variation in warbler population density from plot to plot suggests that more than an incompressible territory is responsible for population regulation. Therefore, like nesting space and nesting material requirements, territories probably require less space for warblers in normal years than does food gathering. Consequently, suitable space is probably the amount of space with an adequate food supply in which the bird is adapted to feed. Direct measurement of the food supply would require a very elaborate sampling scheme. However, measurement of the amount of foliage of the type in which the species has been shown to feed is quite feasible. If the density of breeding pairs of a species is proportional to the amount of foliage in a certain zone, then a census of a plot with twice the volume of this foliage should have twice the number of birds of corresponding species. Since the five

species under consideration feed above 20 feet, only foliage above 20 feet was measured.

Five areas on Mt. Desert Island were censused and measured with this view in mind. All were in predominantly spruce forest, but except for this they were chosen to be as different as possible in order to exhibit as great a range of variation as possible. The volume of foliage above twenty feet was measured as follows. The volume of a cone is proportional to the product of its basal area with its height. The foliage of a spruce tree is roughly a hollow cone with walls of approximately constant thickness. The inner cone may be considered to begin ten feet below the outer. Finally, the basal area of the foliage is proportional to the trunk area. Consequently, the product of the height of foliage in the crown with the basal area of the trunks of the trees will give a figure proportional to the volume of the outer cone. A similar figure for the volume of the inner cone is calculated and the volume of foliage in the hollow shell is obtained by subtraction. The proportion of the volume lying above twenty feet of either the inner or the outer cone is the square of the proportion of the height lying above twenty feet, so that this adjustment is easily made. The number obtained is thus proportional to the desired volume. In practice, the height of foliage in the crown was measured with a rangefinder and the basal area was measured with a "Bitterlich reloscope" (Grosenbaugh 1952).

Plot A was a 3.8 acre section of an open sphagnum bog, the "Big Heath" on Mt. Desert Island. The only trees present were black spruce and tamarack (*Larix laricina*). Trees were very scattered and the highest were between 15 and 20 feet. While typical bog warblers were common, none of the five species considered here was present.

Plot B was a 4 acre strip along the edge of the bog. Red spruce largely replaced black in this plot, the trees occasionally reaching 50 feet in height. The strip was bordered on one side by a road and on the other by the open bog.

Plot C was a 9 acre area along the Hio Truck trail near Seawall on Mt. Desert Island. The forest here was quite mature, trees reaching 70 feet, and was predominantly composed of red spruce, white spruce, and balsam fir, with a higher proportion of white birch than occurred in the other plots.

Plot D was a dense, 4 acre stand of red spruce of moderate age near Southwest Harbor, Maine. Trees reached a height of 60 feet in some places, and had been thinned in part of the plot.

Plot E was the 9 acre stand of white spruce at Bass Harbor Head on Mt. Desert Island in which the observations of 1956 were made. Here the trees reached a height of 70 feet quite frequently, although the mean was nearer 60. This plot apparently originated as an old field stand with numerous, large, low branches. These have died and become covered with a layer of lichens, especially *Usnea*.

For each plot the composition of the warbler population and the volume of the foliage above 20 feet are indicated in figure 10. Here "others" refers to other tree-nesting warblers which fed above 20 feet. It is quite clear that the total tree-nesting warbler population is very nearly proportional to the foliage volume. The abundance of the myrtle warbler is evidently quite constant, only increasing slowly as the volume of foliage increases. This is probably due to its flycatching and ground feeding habits which help to make it less dependent upon the foliage.

Black-throated green warblers were the dominant birds in all mature spruce forest habitats on Mt. Desert Island. As the figure indicates, their abundance was nearly proportional to the foliage volume above 20 feet. Their abundance did fall off slightly in the two plots, C and E, in which very tall trees were present. Black-throated greens seldom use these tall tree tops for feeding, so that the amount of foliage suitable for black-throated greens should be slightly reduced from the amount calculated for plots C and E.

Blackburnians, which require foliage near the tops of the trees, were present in small numbers in both plots which had trees of height greater than 60 feet. A true understanding of their population control on Mt. Desert Island probably cannot be acquired without considering competition with other species. It is reasonable that the blackburnian can only persist where the forest is sufficiently old that the feeding zone of the dominant black-throated green stops well before the tree tops in which the blackburnian prefers to feed.

On Mt. Desert Island, bay-breasted warblers are only common where there are dense growths of lichen-covered lower branches of spruce in the shade of the forest crown. It is in this zone that a large part of their activity takes place and here their sluggish, radially moving, feeding behavior is well suited. This habitat appears when the forest becomes dense and has large trees. Consequently, the bay-breasted warblers only remained permanently in plots D and E. (Two set up territories in plot C but had apparently left by June 8.) Again it appears that this habitat is occupied by the bay-breasted partly because it is not occupied by the black-throated green. In the bud-

worm infested spruce and balsam stands near Ft. Kent, Maine, the bay-breasted warbler was the dominant bird; here they occupied the dense young stands of conifers and black-throated greens were forced to occupy the ridges covered with mixed growths of hemlock and hardwoods. The type of competition in heterogeneous regions mentioned in the first section provides an appropriate explanation for the change in dominance; the forest composition of the whole region is more important than the very local conditions.

Although Cape May warblers did not occupy any of the census plots, observations on their feeding behavior suggest that they would be quite similar to the myrtle warbler as far as dependence on tree foliage is concerned. This is partially confirmed by the fact that of the 18 stations studied in northern Maine, Cape Mays were present in all the lowland ones and dominant only in the fairly open stands with mature trees—a habitat which is unsuitable for the bay-breasted but is quite satisfactory for both myrtle and Cape May.

DISCUSSION AND CONCLUSIONS

In this study competition has been viewed in the light of the statement that species can coexist only if each inhibits its own population more than the others'. This is probably equivalent to saying that species divide up the resources of a community in such a way that each species is limited by a different factor. If this is taken as a statement of the Volterra-Gause principle, there can be no exceptions to it. Ecological investigations of closely-related species then are looked upon as enumerations of the divers ways in which the resources of a community can be partitioned.

For the five species of warbler considered here, there are three quite distinct categories of "different factors" which could regulate populations. "Different factors" can mean different resources, the same resources at different places, or the same resources at different times. All three of these seem important for the warblers, especially if different places and times mean very different—different habitats and different years.

First, the observations show that there is every reason to believe that the birds behave in such a way as to be exposed to different kinds of food. They feed in different positions, indulge in hawking and hovering to different extents, move in different directions through the trees, vary from active to sluggish, and probably have the greatest need for food at different times corresponding to the different nesting dates. All of these differences are statistical, however; any two species show some overlapping in all of these activities.

The species of food organisms which were widespread in the forest and had high dispersal rates would be preyed upon by all the warblers. Thus, competition for food is possible. The actual food eaten does indicate that the species have certain foods in common. The slight difference in habitat preference resulting from the species' different feeding zones is probably more important. This could permit each species to have its own center of dispersal to regions occupied by all species. Coexistence in one habitat, then, may be the result of each species being limited by the availability of a resource in different habitats. Even although the insects fed upon may be basically of the same type in the different habitats, it is improbable that the same individual insects should fly back and forth between distant woods; consequently, there would be no chance for competition. The habitat differences and, equivalently, the feeding zone differences, between blackburnian, black-throated green, and bay-breasted are sufficiently large that this explanation of coexistence is quite reasonable.

The myrtle warbler is present in many habitats in the summer but is never abundant. It has a very large summer and winter range, feeds from the tree tops to the forest floor, and by rapid peering or by hawking. It makes frequent long flights and defends a large territory. Probably it can be considered a marginal species which, by being less specialized and thus more flexible in its requirements, manages to maintain a constant, low population (Figure 10).

The Cape May warbler is in a different category, at least in the region near the southern limit of its range. For here it apparently depends upon the occasional outbreaks of superabundant food (usually spruce budworms) for its continued existence. The bay-breasted warbler, to a lesser degree, does the same thing. During budworm outbreaks, probably because of their extra large clutches, they are able to increase more rapidly than the other species, obtaining a temporary advantage. During the years between outbreaks they suffer reductions in numbers and may even be eliminated locally. Lack's hypothesis, that the clutch is adjusted so as to produce the maximum number of surviving offspring, provides a suitable explanation of the decrease during normal years of these large-clutched species. It may be asked why, if Lack's hypothesis is correct, natural selection favored large clutches in Cape May and bay-breasted. Cheshire's (1954) censuses suggest a tentative answer. During his years of censusing, increases in the bay-breasted warbler population reached a figure of over 300% per year. This probably far exceeds the maximum possible in-
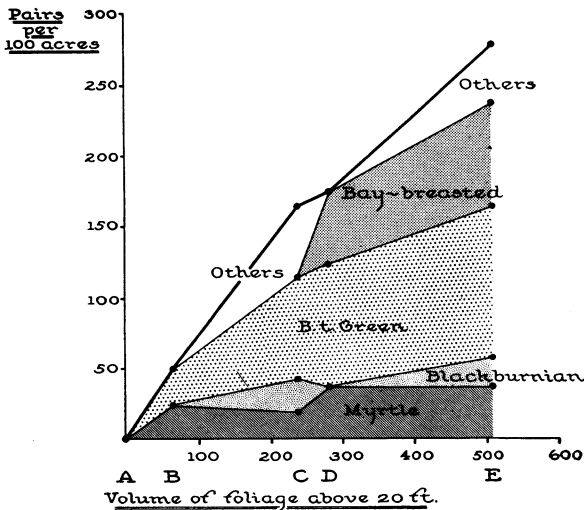
FIG. 10. Composition of the warbler population in plots A, B, C, D, and E. "Others" refers to other warbler species which feed at greater heights than 20 feet above the ground. The units of volume measurement are only proportional to the volume, but each unit roughly equals 1500 cubic feet per acre.

crease due to survival of nestlings raised in that place; probably immigration is the explanation. But if the species with large clutches search for areas in which food is superabundant and immigrate into these regions, then, for the species as a whole, the large clutch may be adapted to the maximum survival of offspring. Cape May and bay-breasted warblers may therefore be considered to be good examples of fugitive species (Hutchinson 1951).

Thus, of the five species, Cape May warblers and to a lesser degree bay-breasted warblers are dependent upon periods of superabundant food, while the remaining species maintain populations roughly proportional to the volume of foliage of the type in which they normally feed. There are differences of feeding position, behavior, and nesting date which reduce competition. These, combined with slight differences in habitat preference and perhaps a tendency for territoriality to have a stronger regulating effect upon the same species than upon others, permit the coexistence of the species.

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