THE UNIVERSITY OF MANITOBA

Feeding Ecology of a Dense

Population of Nesting Yellow Warblers

by

DANIEL G. BUSBY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

January 1978

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A dissertation submitted to the Faculty of Graduate Studies of
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ABSTRACT

The feeding ecology of a dense population of nesting
Yellow Warblers (Dendroica petechia) was studied on the
Delta Beach Ridge, about five km west of Delta, Manitoba
(58° 11' N., 98° 19' W.), during the breeding seasons of
1975 and 1976. Prey availability, prey consumed and foraging
behaviors are described for the adults during the pre-egg,
egg-laying and incubation, nestling and post-nesting periods.

The total numbers and taxonomic composition of the
arthropods available to Yellow Warblers fluctuated irreg-
ularily throughout both breeding seasons. Major changes in
the arthropod fauna were due to massive emergences of adult
chironomids and geometrid larvae. The Chironomidae was the
most abundant group during both breeding seasons and comp-
rised more than half of the available prey. Arthropods were
more numerous in the lower vegetation (0.3-3.0 m) than the
upper vegetation (7.0-9.0 m).

Adult chironomids were the chief prey, comprising 58%
and 56% of the diet in 1975 and 1976, respectively. The
diets of males and females were similar throughout the
breeding seasons; differences in diet are attributed to
feeding locations rather than differential prey selection.
The prey consumed by Yellow Warblers varied temporally
and spatially according to the arthropods available; prey
was taken in proportion to its availability.

Males foraged higher and in taller trees than females. The tree sections used differed between the sexes; males used primarily the upper and outer sections and females used mainly the lower and inner sections. Foraging movements of males were longer than those of females during the egg-laying and incubation period but differences during the remaining periods were not significant. The foraging methods of males and females differed; males gleaned more and hovered less than females. Males foraged in willows more and maples less than females

Rapidly changing prey populations, generalized diet and sexual segregation of the habitat are discussed.

ACKNOWLEDGEMENTS

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INTRODUCTION

The regulation of bird populations in nature has interested population ecologists since Howard's (1920) treatise on territoriality was published. The importance of density-independent factors (eg. climate, disease) versus density-dependent regulation (eg. through competition for food or nest sites, predation) has been debated for the past two decades (see Andrewartha and Birch 1954; Lack 1954, 1966; Kluyver and Tinbergen 1953; Nicholson 1958; Hairston et al. 1960; Murdoch 1966; Slobodkin et al. 1967; Royama 1977). Lack contended that clutch size and ultimately breeding densities are controlled by density-related food conditions (see also Gibb 1960; Yom-Tov 1974). Morse (1976) found an inverse correlation between population density and the standing biomass of food but that physical characteristics of the habitat provide the proximate factor in site selection.

When one species coexists with other similar species that exploit similar resources, for example, food, we might expect its breeding density to be reduced, and its realized niche (Hutchinson 1957) to be compressed, compared to areas where competitors are absent. If, however, this common resource (food) is in unlimited supply both spatially and temporally, then it should be possible for several similar species to live in the area, provided other essential

resources are present.

Such a situation appears to exist on the narrow Delta Beach Ridge that separates the southern shore of Lake Manitoba and the Delta Marsh, Manitoba. Unusually dense populations of seven insectivorous bird species nest in the deciduous habitat on this ridge. The Eastern Kingbird (*Tyrannus tyrannus*), Western Kingbird (*T. verticalis*), and the Least Flycatcher (*Empidonax minimus*) are mainly aerial foragers. The Gray Catbird (*Dumetella carolinensis*), Warbling Vireo (*Vireo gilvus*), Yellow Warbler (*Dendroica petechia*) and Northern Oriole (*Icterus galbula*) comprise a foliage-gleaning guild (see Root 1967).

The Ridge experiences frequent massive swarms of adult midges (Diptera: Chironomidae)(Fig. 1) that emerge from both Lake Manitoba and the Delta Marsh throughout the late spring and summer. Since the appearance of these insects, which settle on the ridge foliage, occurs annually, it appears that an unlimited supply of food exists throughout the breeding seasons of these insectivorous birds.

The objective of the present study is to examine aspects of the feeding ecology of the Yellow Warbler, the most abundant bird on the Delta Beach Ridge, under apparently unlimited food conditions. Since the studies of Gibb (1954, 1960), Lack (1954) and MacArthur (1958), resource partitioning and niche segregation have received much attention, with small insectivorous birds being a popular focal point. Information on foraging behavior, food habits and food

FIGURE 1. Photograph of distant (above) and near

(below) chironomid swarm during a peak of emergence.

availability have been obtained, however few studies have
considered all of these critical aspects to provide a
more detailed description of the factors which influence
the species' feeding ecology.

I studied the feeding ecology of adult Yellow Warblers
with respect to the seasonal availability of prey, the
prey consumed by both sexes, and the foraging tactics of
males and females. These aspects were examined during two
breeding seasons and the relationships between feeding
and the stage of breeding are discussed.

THE STUDY AREA

The study area is a 500 m portion of the Delta Beach
Ridge (Fig. 2), adjacent the University of Manitoba Field
Station, Delta Marsh. This forested ridge is a remnant
shore-line of Glacial Lake Agassiz (Walker 1965, Sproule
1972) built up by north winds, waves and ice (Löve and Löve
1954), and averages 80 m in width. Lake Manitoba extends 180
km to the north of the ridge and the 15,000 ha Delta Marsh
lies to the south, extending about 30 km east-west and eight
km southwards.

Löve and Löve (1954), Walker (1959, 1965), Tamsitt (1962),
Hochbaum (1966) and Sproule (1972) have described aspects
of the ridge. However since vegetational characteristics
vary in different portions of the ridge, a brief description
of the specific study area will be given. All scientific
names follow Scoggan (1957).

Four tree species are common on the study site. Willows
(Salix amygdaloides and S. interior), Manitoba maple (Acer
negundo) and green ash (Fraxinus pennsylvanica) accounted
for 57%, 21% and 20% of the tree flora, respectively. They
provide a forest canopy about 10-14 m in height. The prom-
inent shrubs are elderberry (Sambucus pubens), dogwood
(Cornus stolonifera) and raspberry (Rubus idaeus). Later in
the season the forest floor becomes matted with herbs and
creepers. Most common are stinging nettles (Urtica dioica),
wild cucumber (Echinocystis lobata), Virginia creeper

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FIGURE 2. Illustration of the Delta Beach Ridge with
inset showing location of study area.
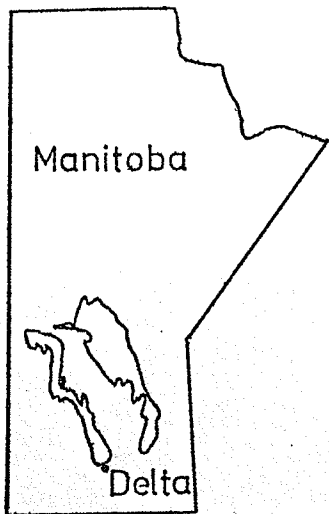
Manitoba

Delta

LAKE
MANITOBA

DELTA
MARSH

(Parthenocissus quinquefolia), hedge bindweed (Convolvulus sepium) and wild hop (Humulus lupulus).

The Delta Marsh is characterized by extensive shallow water which provides optimal habitat for aquatic organisms. Chironomid larvae were the most abundant macroscopic organism, represented by over 30 species with densities of greater than 12,000 larvae / m^2 (Wright 1969). The relative abundance of these species was found to change during the summer as did seven species found in Lake Manitoba (Tudorancia 1974). Each chironomid species has its own non-random period of emergence (Oliver 1971) which accounts for the nearly continual presence of this family throughout the breeding season.

BREEDING SEASON AND DENSITY

In assessing the seasonal changes in feeding habits, prey selectivity and foraging behavior were analysed and discussed relative to four major periods of the breeding season. Period I, the pre-egg stage, spans the period from the return of the first Yellow Warblers in spring, usually males, to the laying of the first egg. Period II includes egg-laying and incubation. Period III, begins with hatching of the first egg and includes the nestling stage. Period IV spans the time from fledging of the first young to fall departure. The dates bounding the periods are given in table 1. Since all nests were not in perfect synchrony, the dates bounding the periods were chosen such that more than 50% of the nests at any given time were at the correct stage, thus facilitating analysis.

Portions of the Delta Beach Ridge support unusually dense breeding populations of Yellow Warblers. Table 2 gives figures presented by or calculated from data given by other authors. In Minnesota, Beer et al. (1956) reported a 0.08 acre island supporting a pair of Yellow Warblers however where three or more pairs occurred together the minimum territory per pair was 0.3 acre.

The density of breeding Yellow Warblers in the present study was determined by counting all active nests in a gridded area (500 m by approximately 80 m) of the beach ridge. Thus the density of 14.5 pairs/ha is minimum since some portions of the ridge were not used by the birds.

TABLE 1. Dates bounding and characteristic activities of
the four periods of the 1975 and 1976 breeding seasons.

Period	Activity	Dates
I	Arrival - first egg	May 9 - June 7
II	Egg laying and incubation	June 8 - June 30
III	First nestling-last fledgling	July 1 - July 19
IV	Post-nesting-fall migration	July 20 - August 21

TABLE 2. Territory size and density of Yellow Warblers.

Density (pairs/ha)	Average territory[1] size (acres)	Location	Study
2.1	1.1 (55)	Michigan	McGeen (1972)
3.5	0.7 (7)	Wisconsin	Young (1949)
5.0	0.5 (1)	Minnesota	Fashingbauer et al. (1957)
5.5-8.2	0.29-0.43 (12)	Ohio	Frydendall (1967)
6.1	0.4 (29)	Iowa	Kendeigh (1941)
8.2	0.3 (46)	Minnesota	Beer et al. (1956)
14.5	0.17 (100)	Delta Beach Ridge	Present Study
29.6	0.08[2]	Delta Beach Ridge	Hochbaum (1971)

[1] Sample size in brackets.

[2] Sample size not available.

THE BIRD

The Yellow Warbler (Aves: Parulidae) is sexually dimorphic in plumage coloration and pattern. The males are bright yellow with prominent chestnut-colored streaks on the breast and abdomen; the females are relatively dull and unstreaked (see Roberts 1955, Godfrey 1966). Males and females are the same size except for the slightly longer wings of males (Table 3). Individuals could therefore be sexed at a distance based on plumage characteristics. All 87 birds sexed by plumage, before being collected for diet analysis, proved correct after dissection.

TABLE 3. Measurements (mean ± 1 SD) of 20 male and 20 female Yellow Warblers collected on the Delta Beach Ridge, June 1 to July 1, 1975 and 1976. Body weight in g, measurements in mm.

	Males	Females
Culmen, from nares[1]	7.69 ± 0.38	7.69 ± 0.30
Bill depth, at nares[1]	3.21 ± 0.13	3.18 ± 0.10
Bill width, at commissural point[1]	5.55 ± 0.35	5.44 ± 0.21
Tarsus[1]	18.30 ± 0.26	18.18 ± 0.36
Wing chord[2]	61.30 ± 2.06	58.50 ± 2.07
Body weight[2,3]	10.29 ± 0.48	11.35 ± 1.29

[1] No significant difference, t-test for samples of equal variance.

[2] P<0.001, same test.

[3] Includes egg-producing and egg-laying females.

METHODS AND MATERIALS

Prey Availability

To determine the availability of food for Yellow Warblers,
arthropods were sampled from the foliage on a one-ha portion
of the beach ridge during both breeding seasons by sweeping
a standard insect sweep net (diam. 37 cm) through Yellow
Warbler foraging habitat. The net was swept swiftly and
firmly through the foliage at heights between 0.3 and 3.0 m.
After 40 such sweeps the contents of the sweep bag were
etherized. The arthropods were separated from the veg-
etation, identified to family, counted, dried to constant
weight and weighed on a Sartorius 2700 balance ($\pm$ 0.001g).
This procedure was repeated in the early morning, after-
noon and evening of every fifth day of the sampling period.
These samples were then averaged and a daily tally of
arthropods was obtained.

In 1976, 40 sweeps were taken from an extension ladder
at a height of 7-9 m on the morning of every second sampling
day. Difficulty was encountered in manoeuvering the sweep
net from this position so the results should be viewed
accordingly. As in the lower sweep samples, individual sweeps
of the net did not overlap. Samples were treated the same
as the lower sweep samples.

Arthropod sampling spanned the period 25 May to 20 August,
1975, and 22 May to 21 August, 1976. Occasionally sampling
was postponed due to inclement weather (high winds, rain).

The arthropods were identified to family and then lumped for analysis into the following groups: Chironomids (midges), Geometrid larvae (inchworms), Culicids (mosquitoes), Coenagrionids (damselflies), Leptocerids (caddisflies), "all other insects" and Arachnids (spiders and mites).

During 1976 an infestation of the forest tent caterpillar (Malacosoma disstria) occurred on the study area. I did not include this insect in the analysis of prey availability since only the very early instars were found in four Yellow Warbler stomachs.

Arthropod samples were obtained twice in 1976 on selected tree species. Each sample consisted of 40 sweeps taken on several trees of each species. The samples were treated like the regular sweep samples.

Diet

To describe the diet of adult Yellow Warblers, birds were collected, mainly by shooting, in an area adjacent the study area. Birds taking food for the female or young, identified by prey visible in the bill, were not taken. Three specimens, including at least one of each sex, were taken at five-day intervals during the breeding seasons. Each collection was made the day after the arthropods were sampled. Twenty-five males and 22 females were taken between 26 May and 19 August 1975; 20 males and 20 females were taken between 22 May and 17 August 1976.

The stomachs and esophagi of each individual were removed

immediately after collection and stored in 70% ethanol.
Post-mortem digestion was therefore minimized (see Van
Koersveld 1951). The food samples were examined later in
the laboratory under a variable power microscope.

Intact prey were few in the samples. Certain fragments
(wings, anntenae, etc.) were thus sorted and included in
the totals for each sample. Food items were identified to
family and lumped into the same seven groups as the sweep
net samples. Thus selectivity in feeding could be determ-
ined by comparing the proportion of food items in the
environment with that in the stomachs.

The similarity of male and female diets over the breeding
seasons was ascertained using Morisita's index of overlap
(Horn 1966); a value of zero suggests minimal overlap and
a value of one suggests strongly similar diets.

Foraging Behavior

To describe various aspects of foraging behavior, Yellow
Warblers were observed with 7 X 35 wide-angle binoculars
and the details were recorded with a portable tape record-
er. Details of activities were worded to permit timing
with a stop watch when playing back the recordings. Phys-
ical measurements were made with a 100 m tape and a hand-
made inclinometer which was about 95% accurate. The bird's
sex, its foraging height, the section of the tree where it
was foraging (Fig. 3), the time spent foraging in that
section, the tree or shrub height and the foraging methods

FIGURE 3. Divisions of trees and shrubs used in
analysis of tree sections used by foraging male
and female Yellow Warblers.
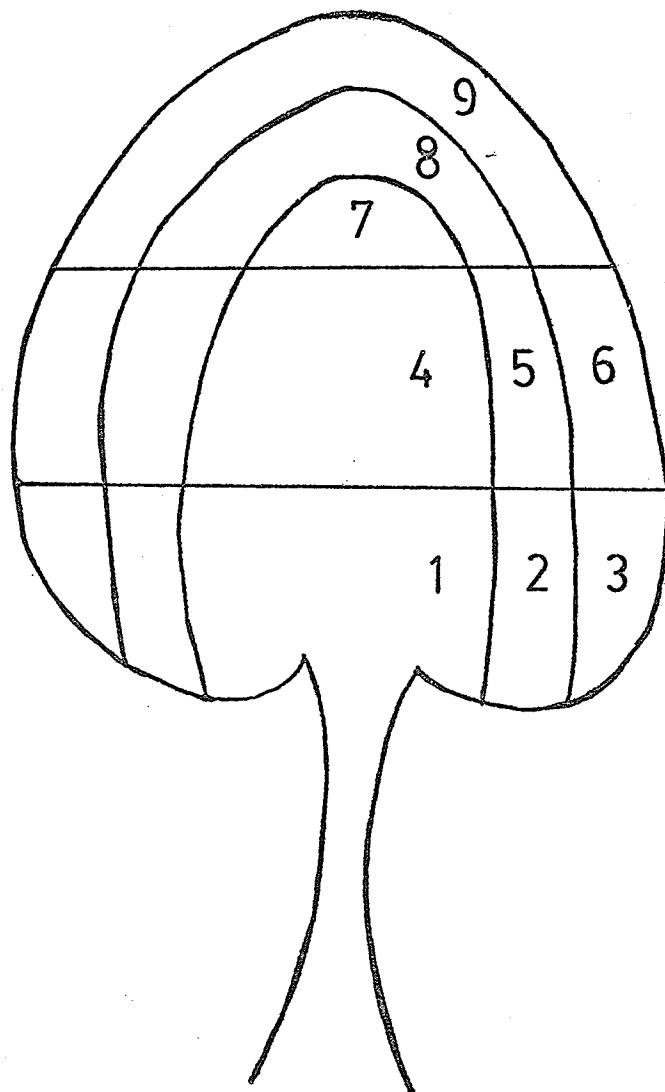
used were recorded. When the bird moved from one tree section to another (perhaps in another tree), this distance was recorded.

Foraging behavior was studied on at least two days in every five-day period throughout 1976. Observations were confined to a 500 m section of the beach ridge. About 25,000 seconds of foraging observations were made. A random method of approach to the study area was used to reduce bias of particular birds or particular areas of the ridge. The Kolmogorov-Smirnov two-sample test for independent samples was used for analysis of foraging data.

RESULTS

Prey Availability

The numbers of arthropods fluctuated irregularly through-
out the 1975 and 1976 breeding seasons (Figs. 4 and 5).
They were generally greatest in early June and mid-to late
July. In 1975, the major fluctuations resulted from the
appearance of adult chironomids (Fig. 4). Minor fluctuat-
ions were caused by an increase of arachnids and "all other
insects". In 1976, chironomid adults and geometrid larvae
caused the major fluctuations (Fig. 5). Minor changes
resulted from fluctuations in the "all other insects" group.

Chironomidae was the most abundant group during both
breeding seasons and comprised more than half of the avail-
able prey (Table 4). These insects were an extremely vis-
ible component of the arthropods on the foliage. During
peaks of emergence their weight on the foliage caused small
branches to bend. Mating swarms of chironomids, especially
at sunrise and sunset, were very conspicuous and audible.
Geometrid larvae were an important component of the arth-
ropod fauna during June in both years. Culicids, leptocerids
and coenagrionids formed a minor component of the samples.
Arachnids formed a minor but regular part of the prey avail-
able while the "all other insects" group was the second most
abundant group.

Generally, arthropods were more numerous at the 0.3-3.0 m

FIGURE 4. Composition of arthropod sweep samples, 1975.
Top of each bar represents the total number of arthropods
in the sample; percent composition of each sample is
represented within each bar.
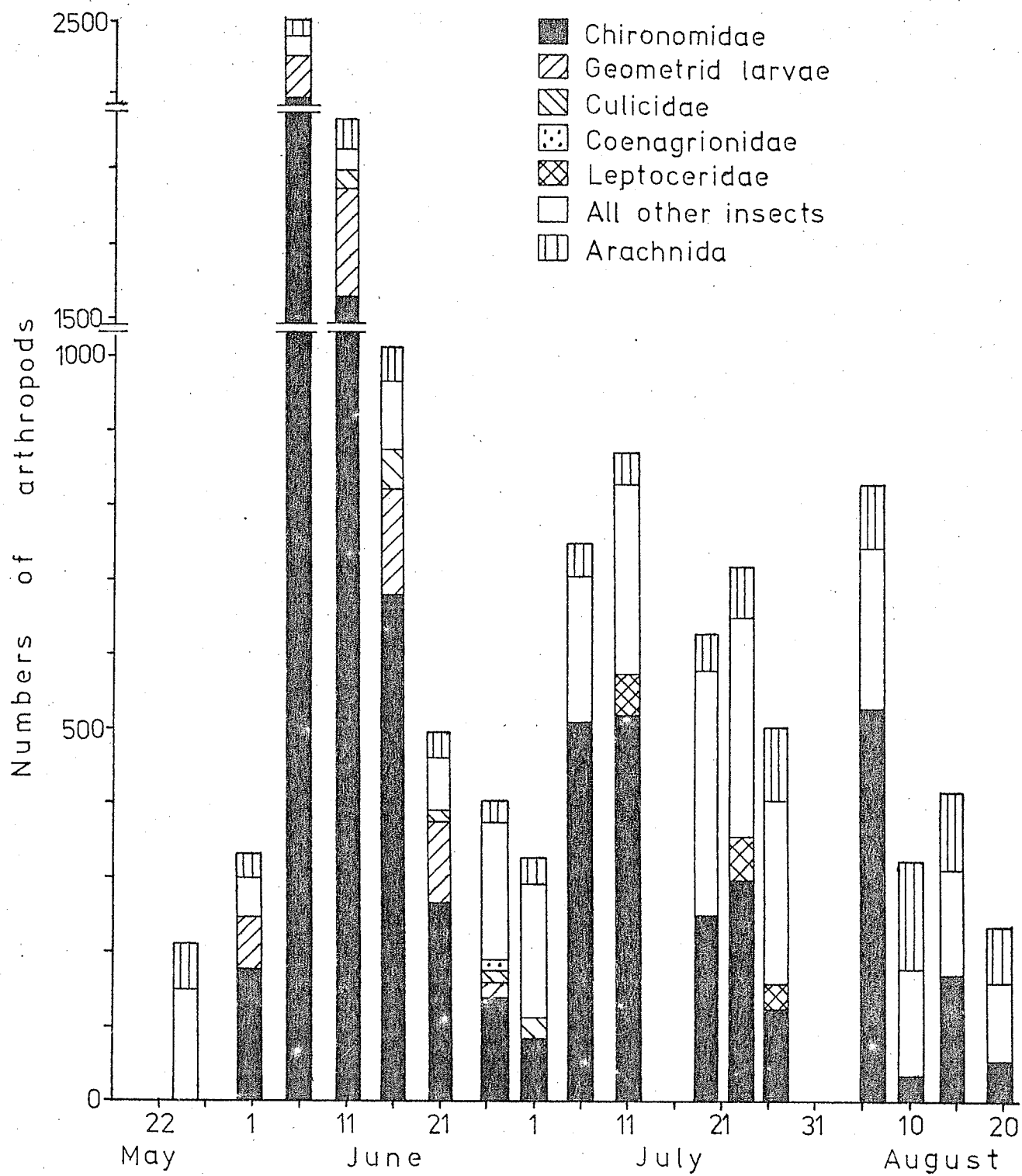
FIGURE 5. Composition of arthropod sweep samples, 1976.

   Top of each bar represents the total number of arthropods

   in the sample; percent composition of each sample is

   represented within each bar. Ledgend as in Fig. 4.
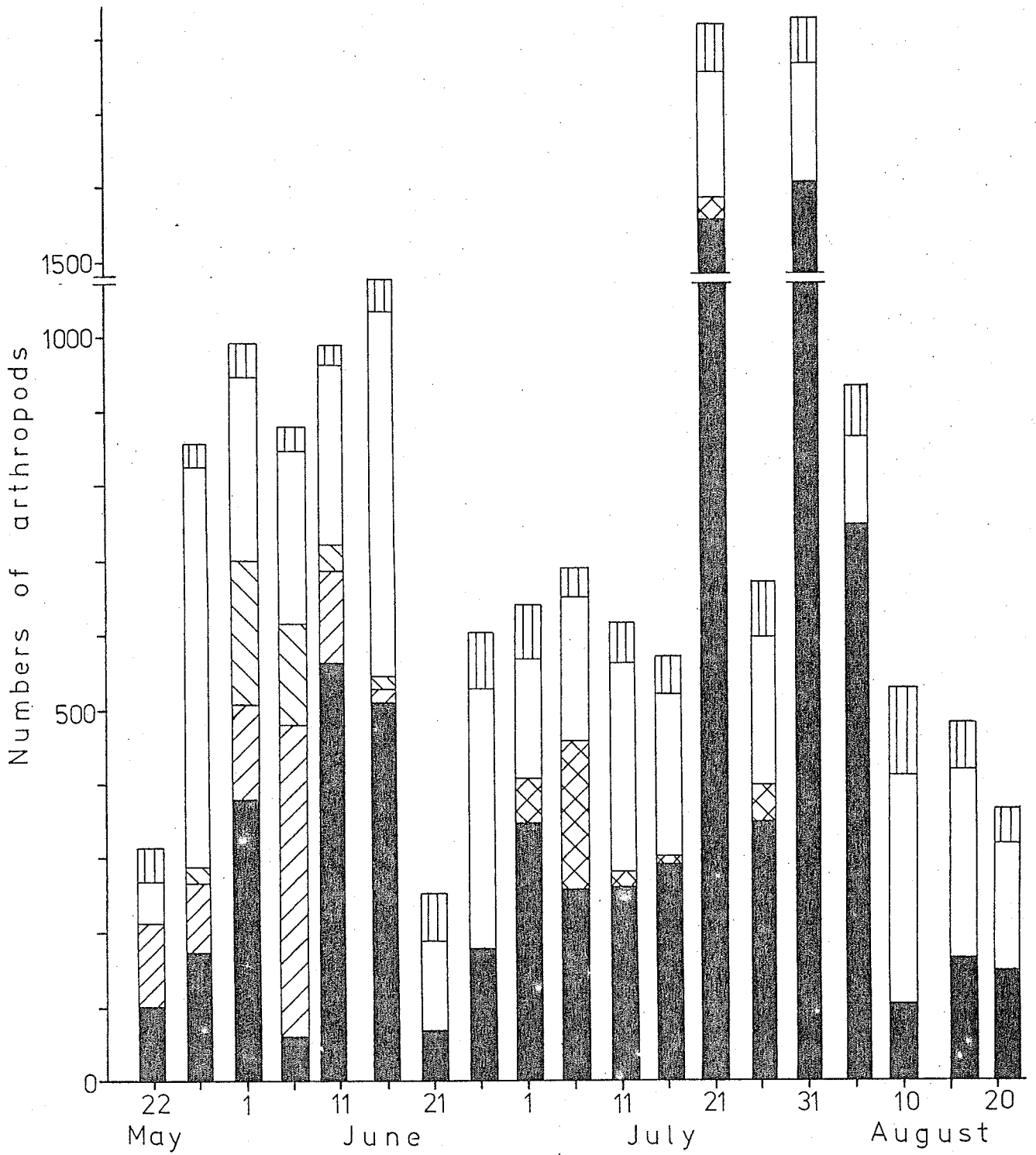
TABLE 4. Percent composition by numbers of arthropod fauna
in the sweep net samples in 1975 and 1976.

Arthropod group	1975	1976
Chironomidae	63.5	52.2
Geometrid larvae	4.5	6.1
Culicidae	1.3	2.8
Coenagrionidae	0.1	0.2
Leptoceridae	1.2	2.5
"All other insects"	21.6	29.6
Arachnida	7.8	6.6

levels than at the 7-9 m level (Fig. 6). However during period I and early period II geometrid larvae were more numerous at the higher level as were chironomids in period II. The number of families identified was almost invariably greater at the lower level than the higher level (Fig. 7).

There was a marked difference in the distribution of arthropods on the foliage of the three major tree species in 1976. Ashes harboured fewer arthropods than maples (X^2= 102.4; 1 df; $P < 0.001$) and willows (X^2= 86.4; 1 df; $P < 0.001$). Maples and willows were similar (X^2= 0.70; 1 df; NS).

In 1975 and 1976, 83 and 78 families of insects were identified, respectively. In both years approximately six families could not be identified past order, however these groups were a very minor component of the insect fauna.

Diet

Thirty-four and 38 families of insects were found in the diet of Yellow Warblers in 1975 and 1976, respectively (Appendix 1). In addition, arachnids, a few diptera, coleoptera and lepidoptera which were found in the samples were not identified further. All families of insects eaten by Yellow Warblers were also found in the sweep net samples.

Adult chironomids were the chief prey comprising 58% and 56% of the diet in 1975 and 1976, respectively (Table 5). "All other insects" was second most numerous in the diet comprising about 30% in each year. The remaining 12% and

FIGURE 6. Relative abundance (numbers) of arthropods
at 0.3-3.0 m (solid lines) and 7.0-9.0 m (dashed lines),
Delta Beach Ridge, 1976.
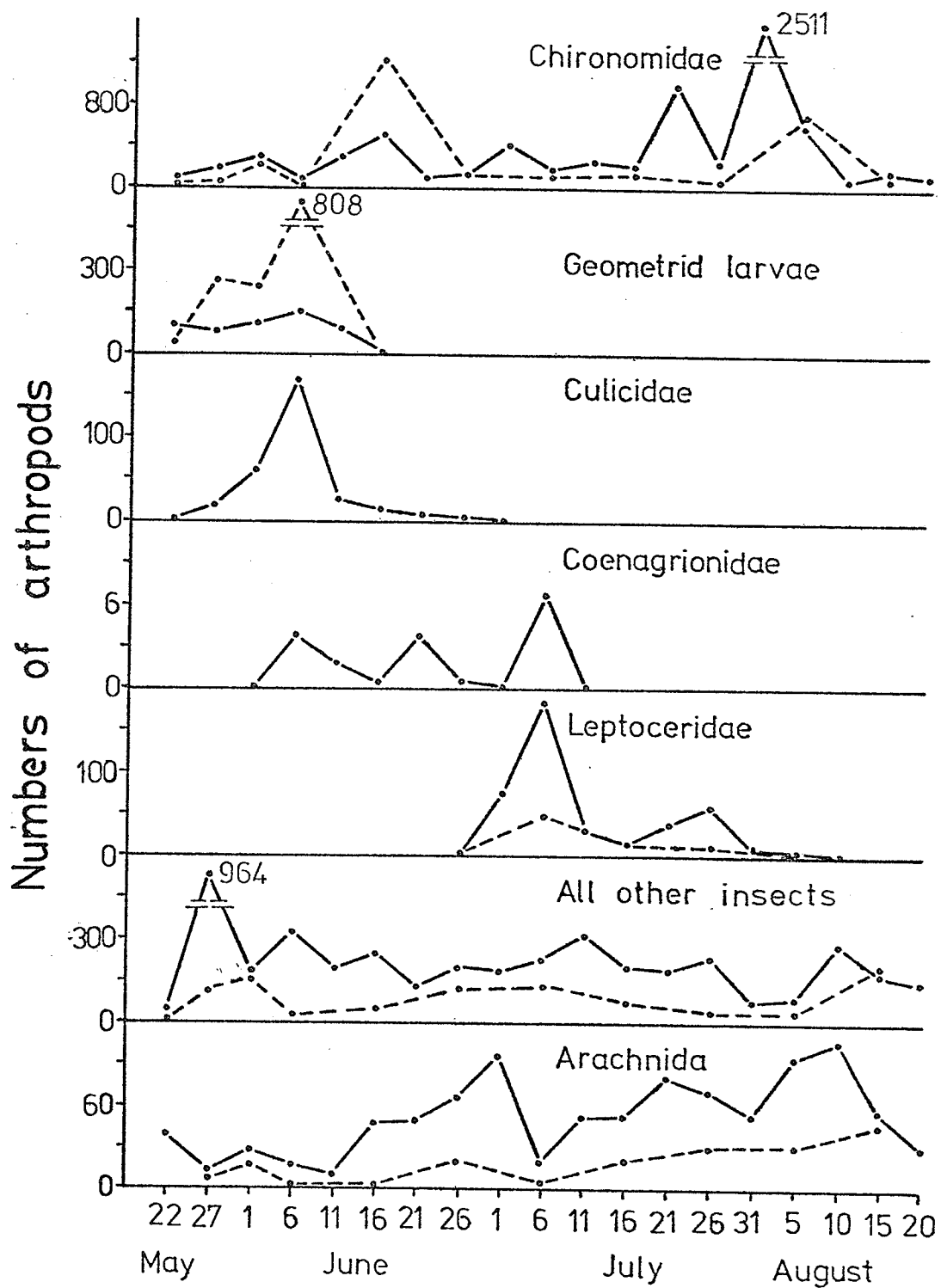
FIGURE 7. Relative abundance (numbers) of arthropod
families identified from sweep samples at 0.3-3.0
m (solid lines) and 7.0-9.0 m (dashed lines), Delta
Beach Ridge, 1976.
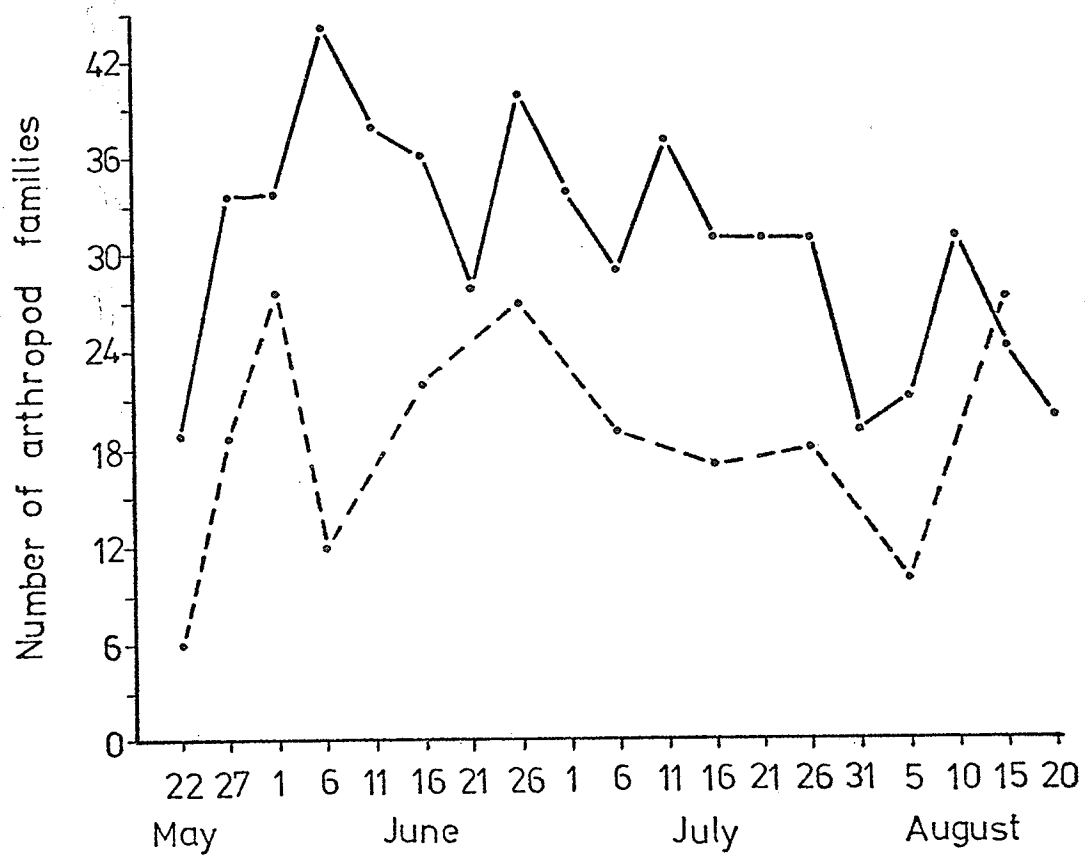
TABLE 5. Percent composition by numbers of the arthropod
fauna eaten by Yellow Warblers in 1975 and 1976.

Arthropod group	1975	1976
Chironomidae	58.0	55.7
Geometrid larvae	10.7	6.5
Culicidae	-	3.5
Coenagrionidae	-	1.5
Leptoceridae	-	1.3
"All other insects "	30.5	29.4
Arachnida	0.8	2.1

14% of the diet in 1975 and 1976, respectively, was comprised of the remaining groups.

The results of Morisita's index of overlap, calculated on frequency of occurence of families in the diet, suggest that males and females took very similar prey (Table 6). The general breeding season values of 0.97 and 0.88 for 1975 and 1976, respectively, approach the maximum theoretical value of approximately 1.0 (Morisita 1959). This indicates strong similarity and therefore the diets of males and females were combined in the analysis of diet and prey availability.

The overlap value in both years for period II is lower than that of the other three periods in each year. Period IV, 1975, is also low. However all values except period II, 1976, are high enough to suggest strongly similar diets in the respective periods. The exception is attributed to females taking a high proportion of chironomids and males taking more geometrid larvae.

Although male and female diets were similar, two exceptions are evident. Females took more chironomids in both years ($X^2 = 26.0$; 1 df; $P < 0.001$, 1975; $X^2 = 53.0$; 1 df; $P < 0.001$, 1976) and males took more geometrid larvae in both years ($X^2 = 7.80$; 1 df; $P < 0.01$, 1975; $X^2 = 10.1$; 1 df; $P < 0.005$, 1976).

I did not take measurements of the size of prey eaten by males and females, however there was no evidence of differential prey-size selection by the sexes. The smallest arth-

TABLE 6. Morisita's (1959) index of overlap for the diets
of male and female Yellow Warblers in 1975 and 1976.

			Period		
Year	I	II	III	IV	Combined
1975	1.00	0.72	0.99	0.75	0.97
1976	0.70	0.40	0.99	0.99	0.88

ropods (mites) and the largest arthropods (damselflies) were found in both male and female stomachs. Damselflies were taken by females more than males ($X^2 = 5.4$; 1 df; $P < 0.05$, both years combined) however these insects were less abundant higher in the canopy (Fig. 6) where males foraged most frequently (see foraging behavior). Furthermore, since the sexes take similar prey families (index of overlap) and since different members of each family are of similar size, prey-size selection should be similar.

Prey Availability and Diet

In general, Yellow Warblers eat prey in proportion to its availability (Figs. 8a and 9a). Spearman rank correlation coefficients were significant for both breeding seasons ($r_s = 0.86$, $P < 0.01$, 1975; $r_s = 0.99$, $P < 0.001$, 1976). However when the individual periods of the two breeding seasons are considered there is no simple relationship between food available and food eaten. Period I shows the largest discrepancies; in 1975 (Fig. 8b) chironomids were taken in proportions less than their availability and in 1976 (Fig. 9b) the opposite prevails. In 1975, geometrid larvae were eaten in proportion to their availability whereas in 1976 they were taken in proportions less than what was available.

A closer relationship exists between prey available and prey taken in the remaining periods. However in all periods

FIGURE 8. Percent composition by numbers of prey available and prey used by Yellow Warblers in 1975. A, all periods; B, period I; C, period II; D, period III; E, period IV.

Chironomidae
Geometridae
Culicidae
Coenagrionidae
Leptoceridae
All Other Insects
Arachnida
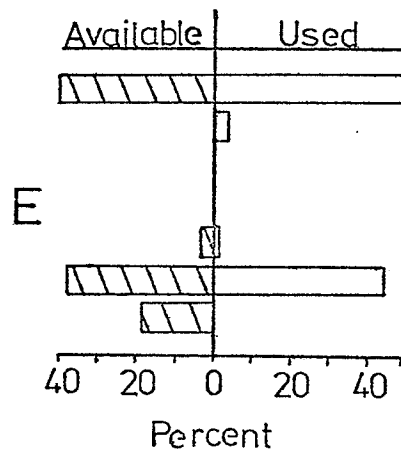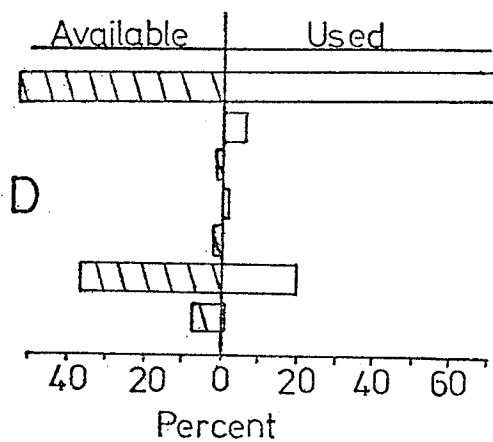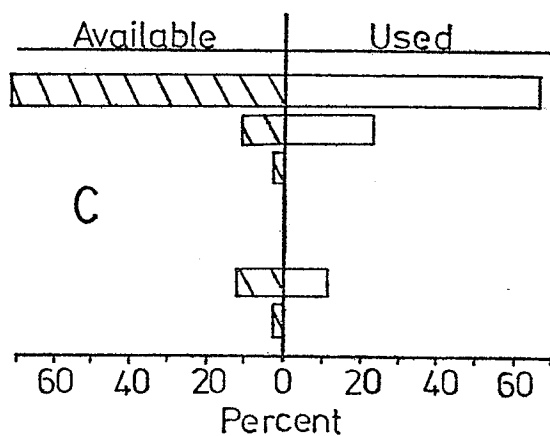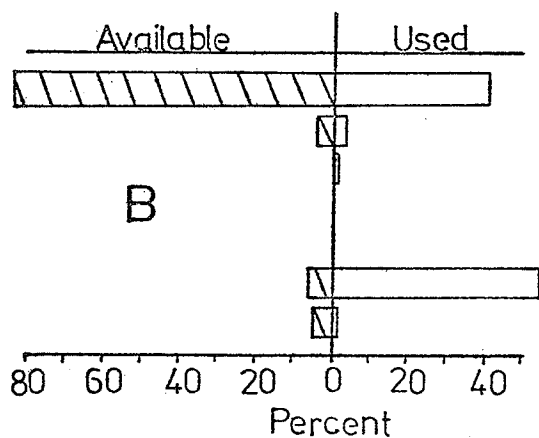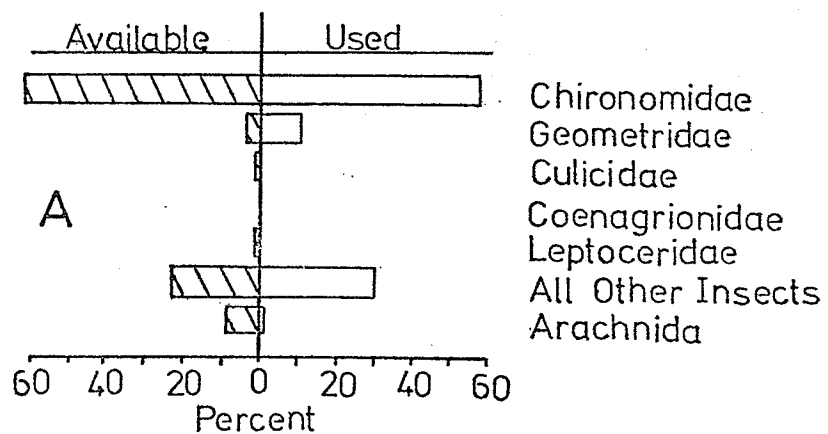
FIGURE 9. Percent composition by numbers of prey
available and prey used by Yellow Warblers in 1976.
A, all periods; B, period I; C, period II; D, period
III; E, period IV.

Available | Used

Chironomidae
Geometridae
Culicidae
Coenagrionidae
Leptoceridae
All Other Insects
Arachnida

A

40 20 0 20 40
Percent

B

20 0 20 40
Percent

C

40 20 0 20 40
Percent

D

40 20 0 20 40 60
Percent

E

60 40 20 0 20 40 60
Percent
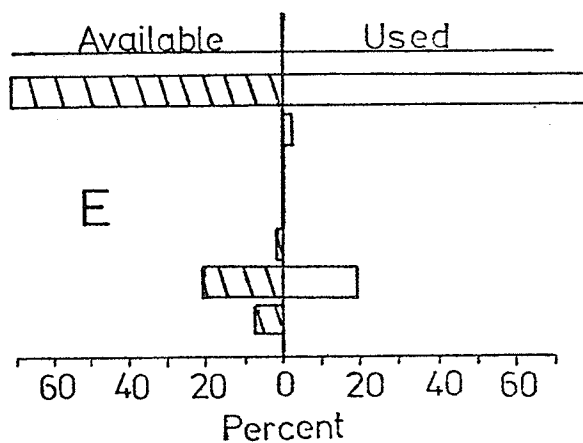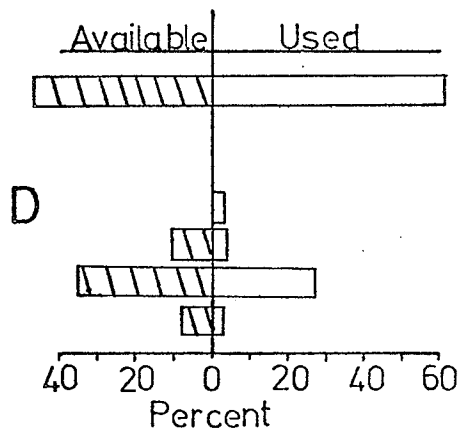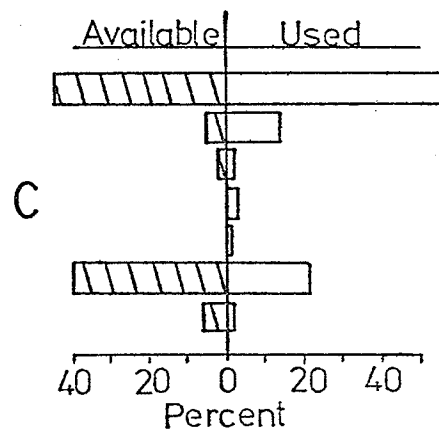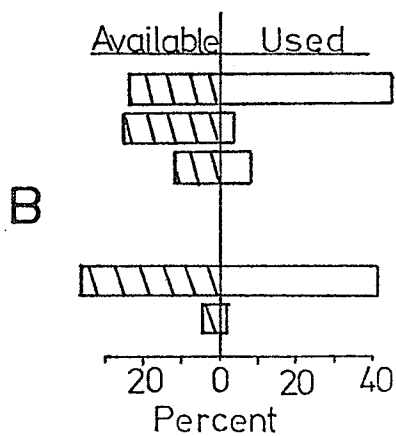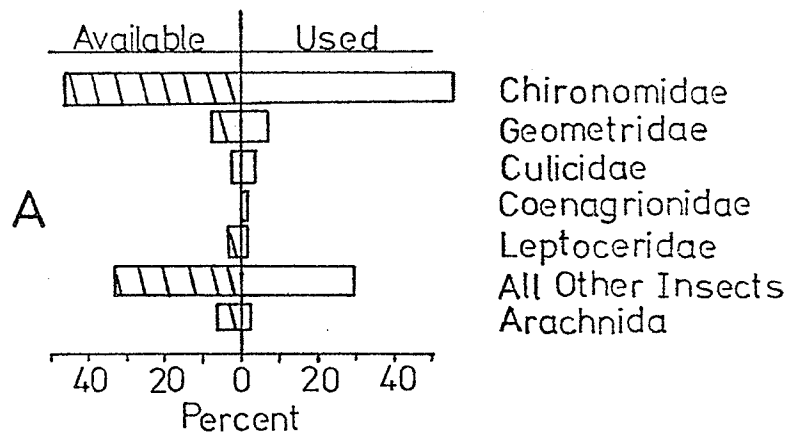
arachnids were eaten in lesser proportions relative to what was available.

Foraging Behavior

Male and female Yellow Warblers foraged at different heights (P < 0.001) during the breeding season (Fig. 10a). Seventy-three % of the foraging observation time for females was at a height of five m or less; for males only 37% occurred at that level. The foraging height of males and females differed greatly during period I (P < 0.001); males foraged higher than females (Fig. 10b).

Males foraged lower in periods II and III (Fig. 10c and d) than in period I; females in periods II and III remained at heights similar to those in period I. Males and females once again foraged at different heights in both periods II and III (P < 0.001, both periods); the males foraged higher than females. In period IV, both sexes foraged higher (Fig. 10e) than during the previous periods but males still foraged higher than females (P < 0.001).

The height of the trees where foraging occurred differed (P < 0.001) between the sexes (Fig. 11a). Sixty-eight % of the female observation time occurred in trees nine m or less whereas only 48% of male observation time occurred there. In periods I, II and IV (Figs. 11b, 11c and 11e, respectively) males foraged in higher trees (P < 0.001, all periods). In period III (Fig. 11d) the trend is less distinct, although females still foraged in lower trees (P < 0.001).

FIGURE 10. Foraging height of males (dashed lines) and
females (solid lines). Number of seconds is total
time of observations on each sex. A, all periods;
B, period I; C, period II; D, period III; D, period IV.
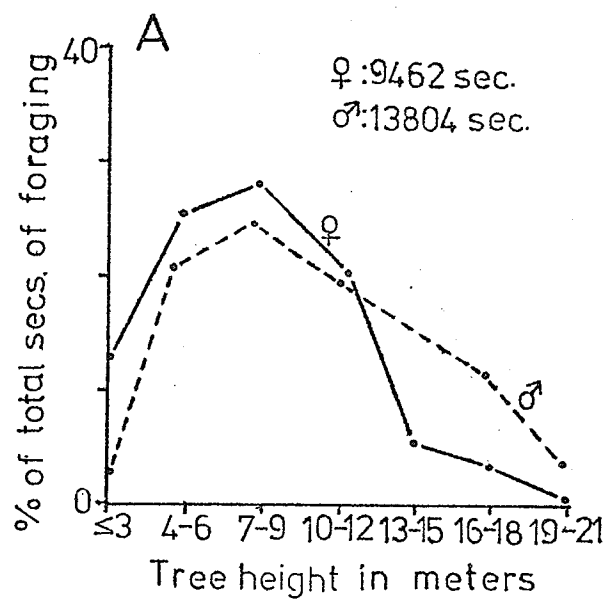
FIGURE 11. Heights of trees used by males (dashed lines) and females (solid lines). Number of seconds given is total time of observations on each sex. A, all periods; B, period I; C, period II; D, period III; E, period IV.

A

♀ : 9483 sec., X̄=4.4 m
♂ : 13903 sec., X̄=7.1 m

% of total secs. of foraging

50

♀

♂

0

0-2   3-5   6-8   9-11 12-14 15-17

Height in meters

B

50

♀ : 1463 sec., X̄=4.0 m
♂ : 4782 sec., X̄=9.2 m

0

0-2   3-5   6-8   9-11 12-14 15-17

C

50

♀ : 5066 sec., X̄=4.3 m
♂ : 5517 sec., X̄=6.1 m

0

0-2   3-5   6-8   9-11 12-14 15-17

D

50

♀ : 2166 sec., X̄=4.3 m
♂ : 2664 sec., X̄=5.4 m

0

0-2   3-5   6-8   9-11 12-14 15-17

E

50

♀ : 788 sec., X̄=6.8 m
♂ : 940 sec., X̄=8.0 m

0

0-2   3-5   6-8   9-11 12-14 15-17
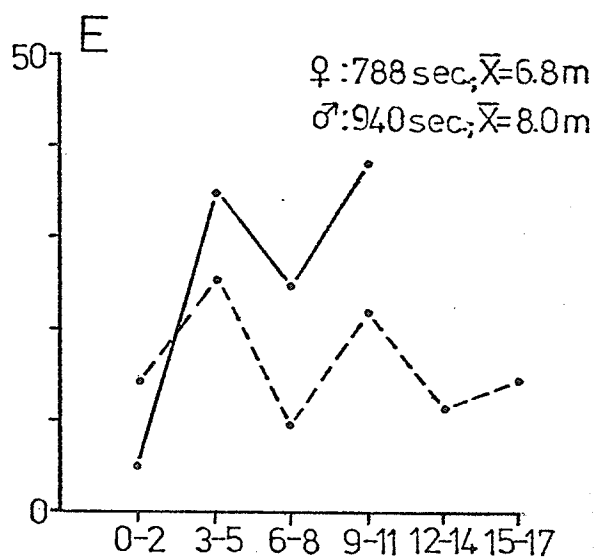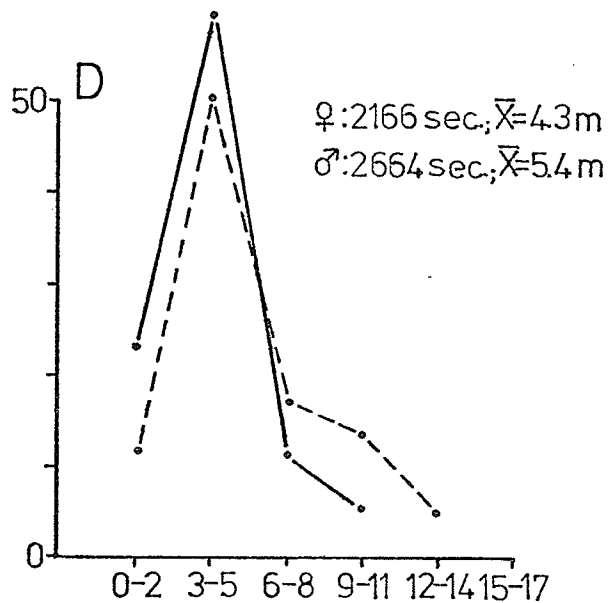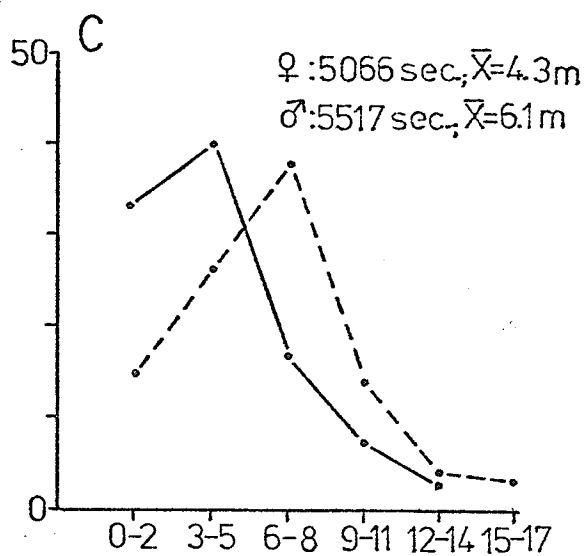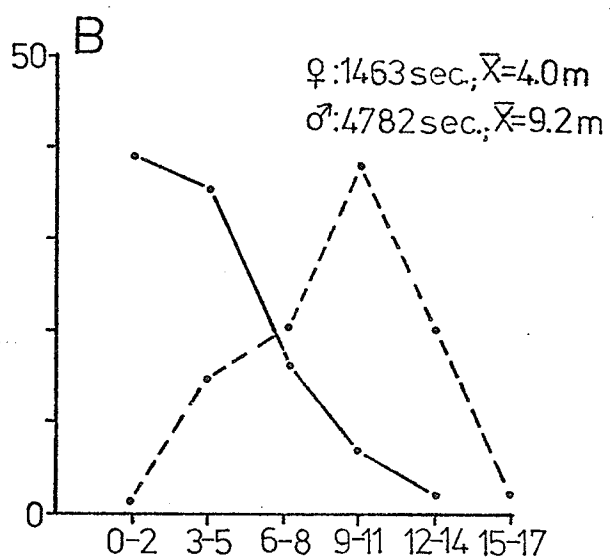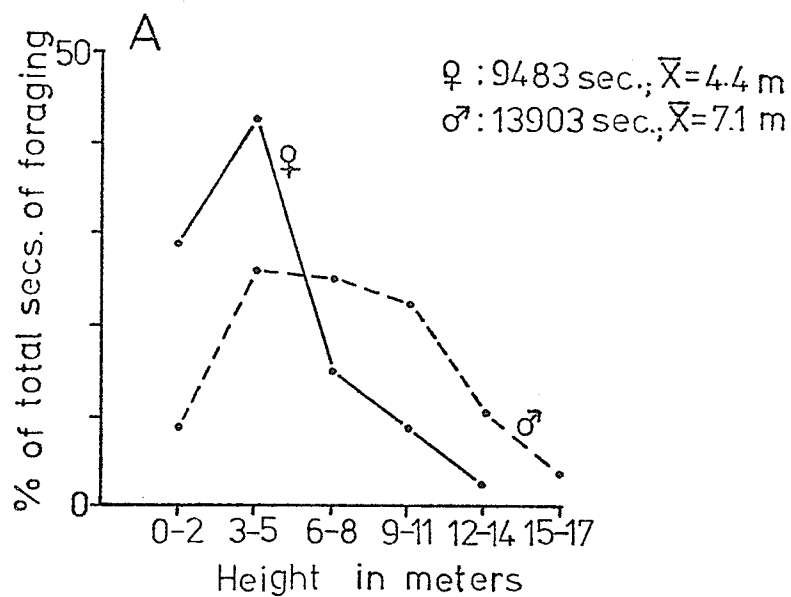
The tree section where foraging occurred differed
(P < 0.001) between males and females. Fifty-two % of the
female observation time occurred in section five or less.
For males, the equivalent figure was only 29% (Fig. 12a).
In the first two periods males foraged in the upper and
outer sections and females foraged in the lower and inner
sections (Fig. 12b and c)(P < 0.001, both periods). In the
last two periods (Fig. 12d and e) there is more overlap
in the sections used however the differences are still
significant (P < 0.001, both periods).

The distance moved by foraging birds differed between
males and females (P < 0.001). Eighty-eight % of female
movements were ≤3 m compared to 60% of male movements.
(Fig. 13a). Considered separately, however, movements by
males and females in period II (Fig. 13c) showed signif-
icant differences (P < 0.001). In the remaining periods the
differences were not significant.

The foraging methods of males and females differed
(P < 0.001) for the breeding season. Females gleaned and
hovered 71% and 26% of the time, respectively; the males
85% and 11%, respectively (Fig. 14a). However when con-
sidered separately, only periods II and III (Fig. 14c and d)
differed significantly (P < 0.05, both periods). Periods I
and IV (Fig. 14b and c) showed non-significant differences.
In all periods females gleaned less often and hovered more
often than males.

Males foraged in different tree species than females

FIGURE 12. Section of tree used by males (hatched bars) and females (solid bars). Number of seconds given is total time of observations on each sex. A, all periods; B, period I; C, period II; D, period III; E, period IV.

A ♀ :9610 sec. ♂:13862 sec.

% of total secs. of foraging

30

1 2 3 4 5 6 7 8 9

Tree   section

♀ =
♂=

B ♀ :1487 sec. ♂:4284 sec.

40

0

1 2 3 4 5 6 7 8 9

C ♀ :5170 sec. ♂:5930 sec.

30

0

1 2 3 4 5 6 7 8 9

D ♀ :2165 sec. ♂:2707 sec.

30

0

1 2 3 4 5 6 7 8 9

E ♀ :798 sec. ♂:941 sec.

30

0

1 2 3 4 5 6 7 8 9
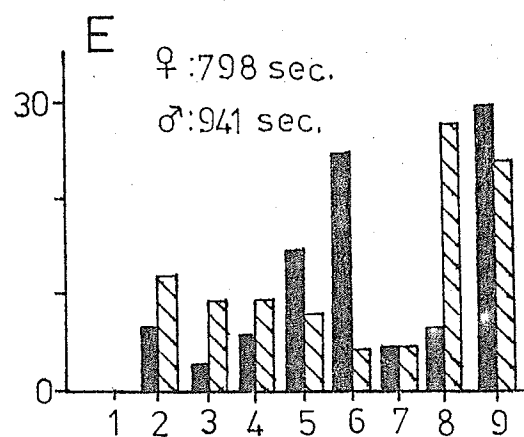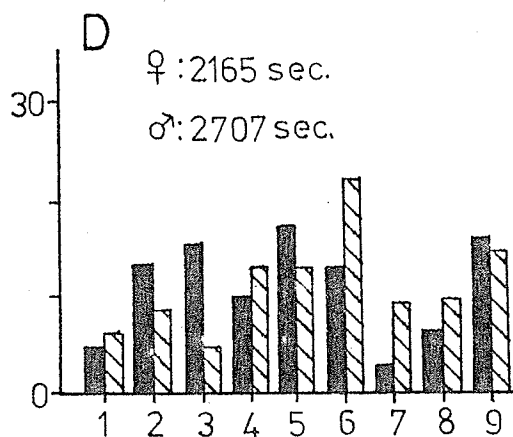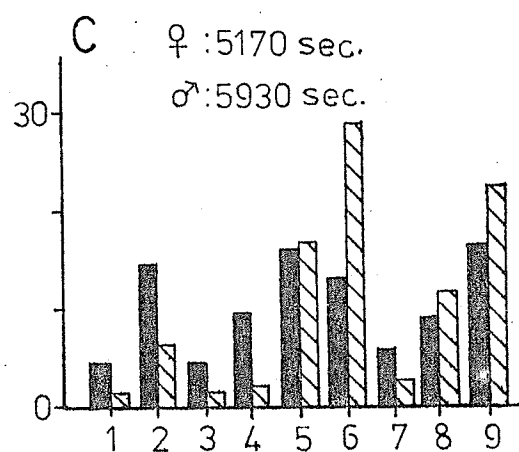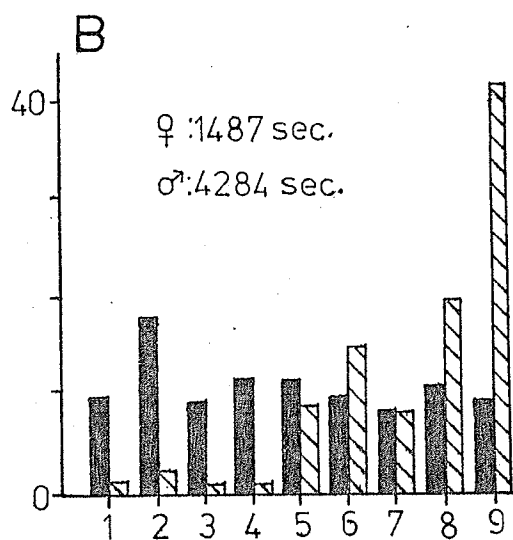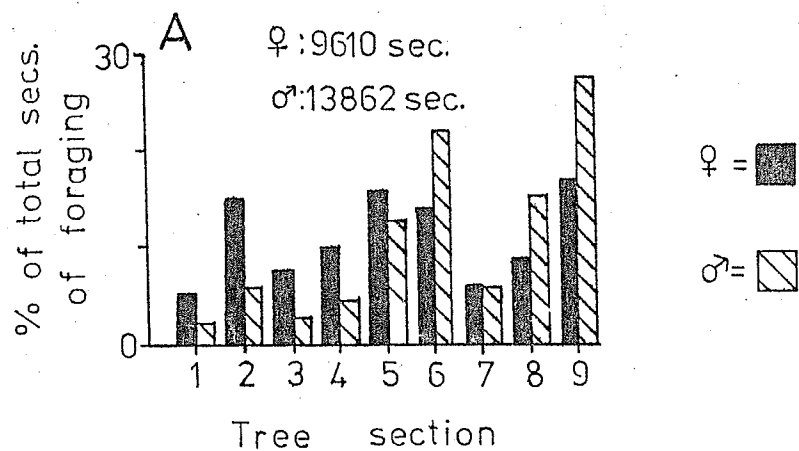
FIGURE 13. Length (m) of foraging movements of males
(dashed lines) and females (solid lines). Number of
observations of movements given after sex symbol.
A, all periods; B, period I; C, period II; D, period
III; E, period IV.
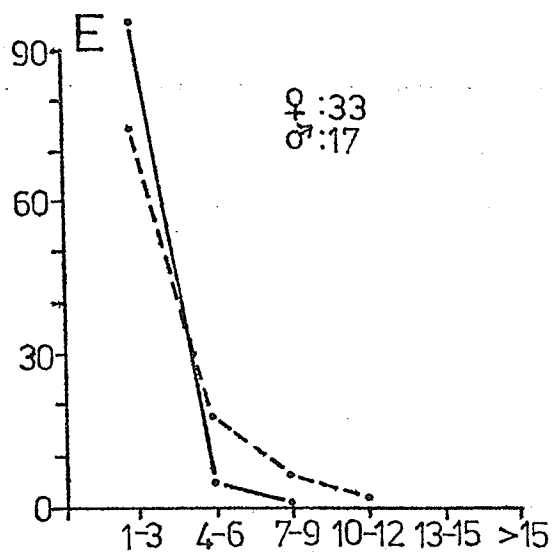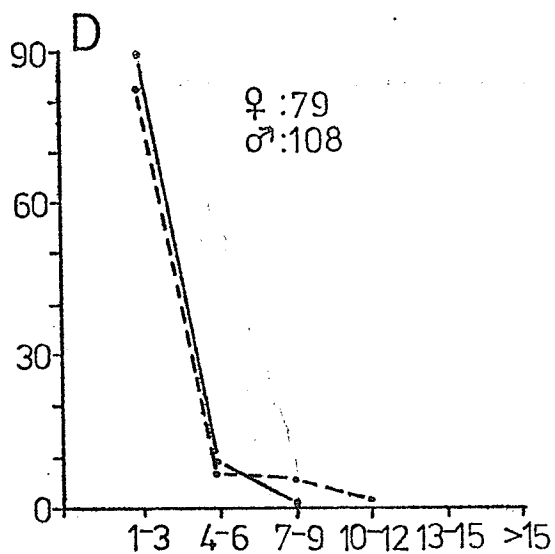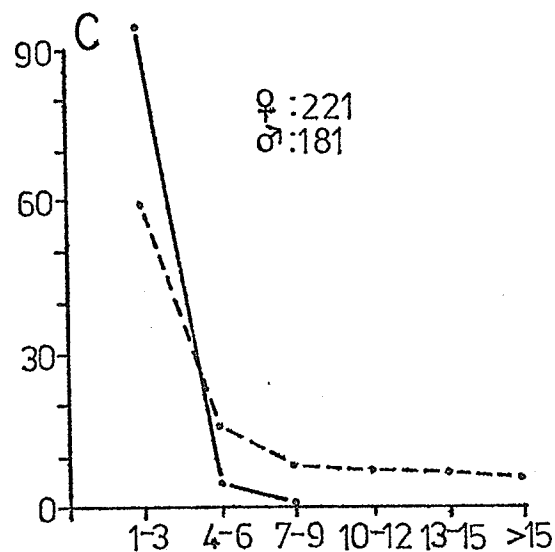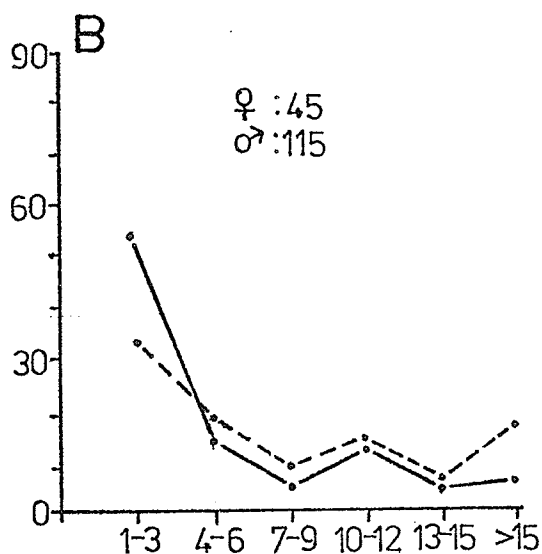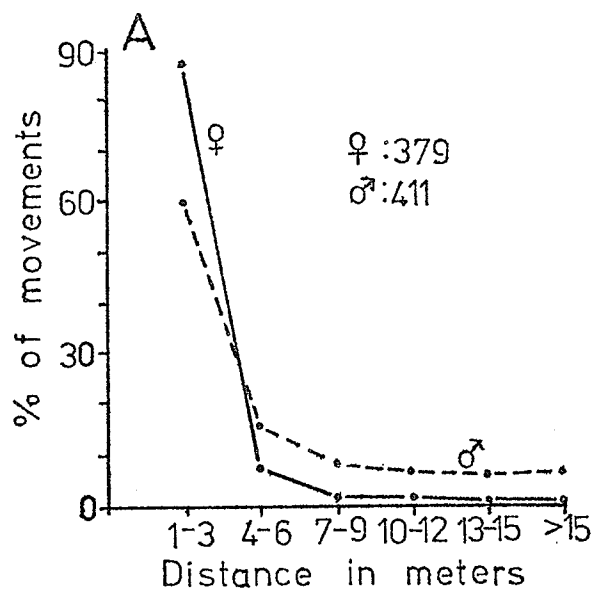
FIGURE 14. Foraging methods used by males (hatched bars) and females (solid bars). Number of observations of foraging manoeuvers given after sex symbol. A, all periods; B, period I; C, period II; D, period III; E, period IV.
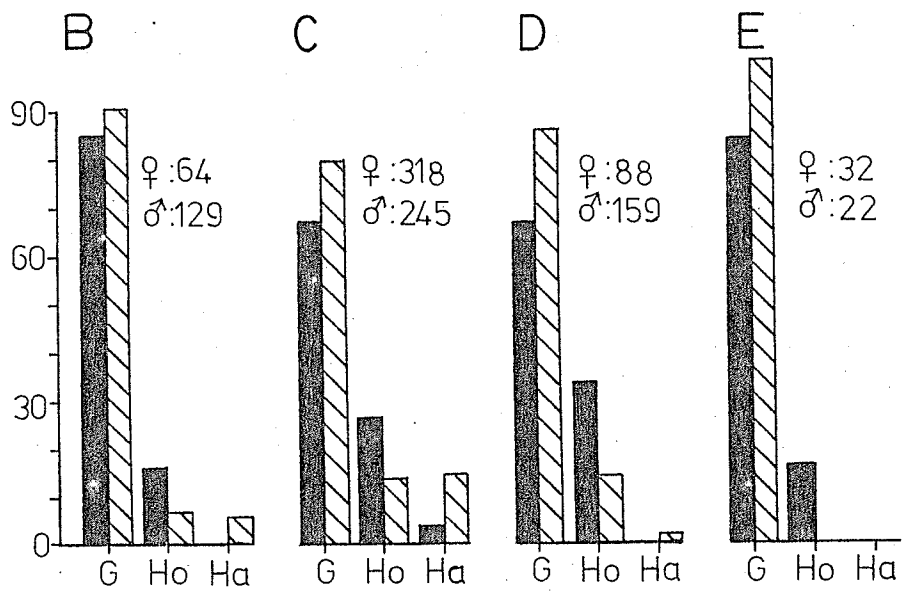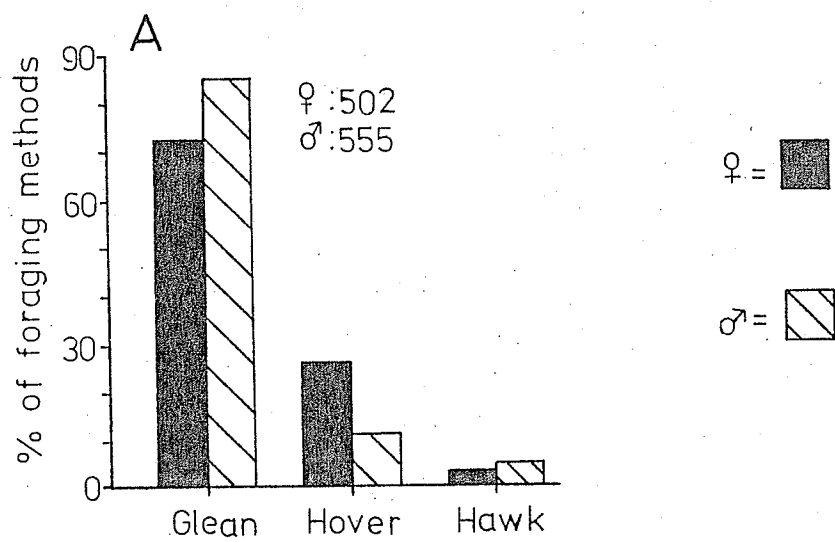
(P < 0.001) during the breeding season (Fig. 15a). In period I (Fig. 15b), females foraged in ashes more and willows less than males (P < 0.001). In the remaining periods (Fig. 15c, d and e) females used maples more and willows less than males (P < 0.001, all periods).

Females foraged more in shrubs than did males ($X^2 = 50.71$; 1 df; P < 0.001).

FIGURE 15. Tree species in which males (hatched Bars)
and females (solid bars) foraged. Number of seconds
given is total time of observations on each sex.
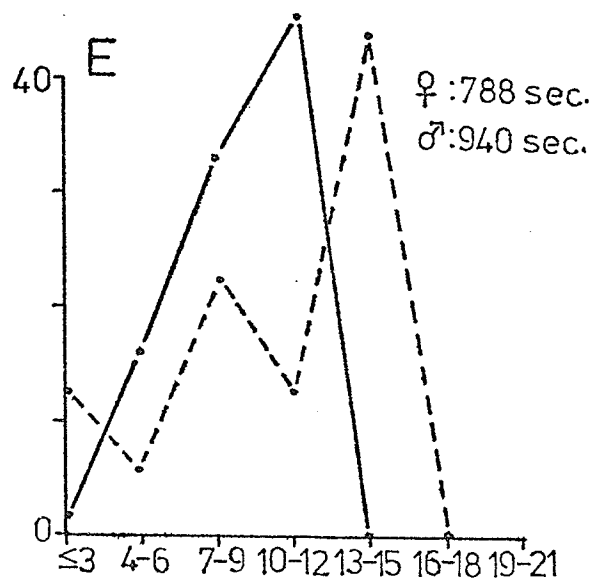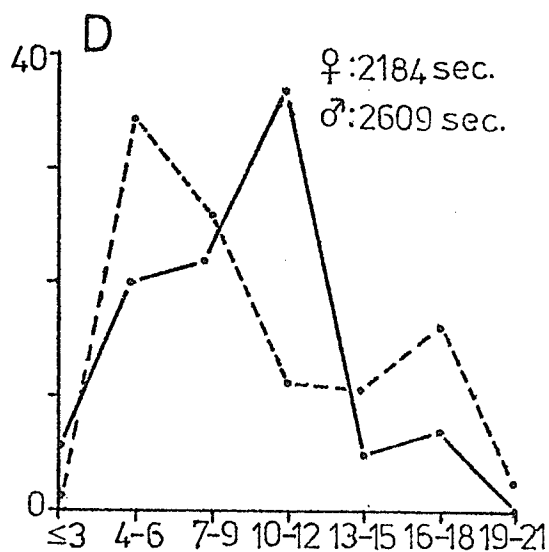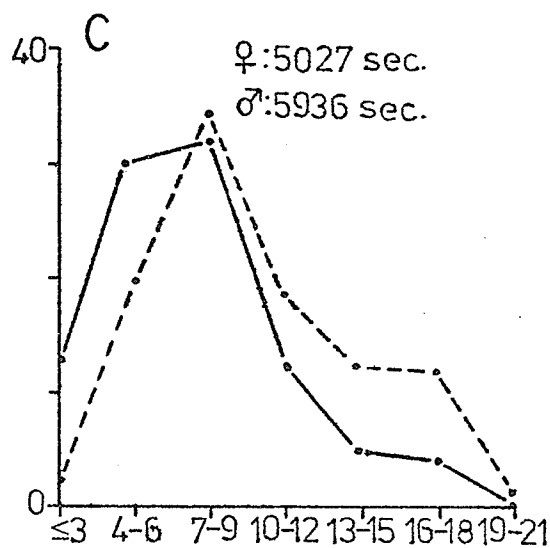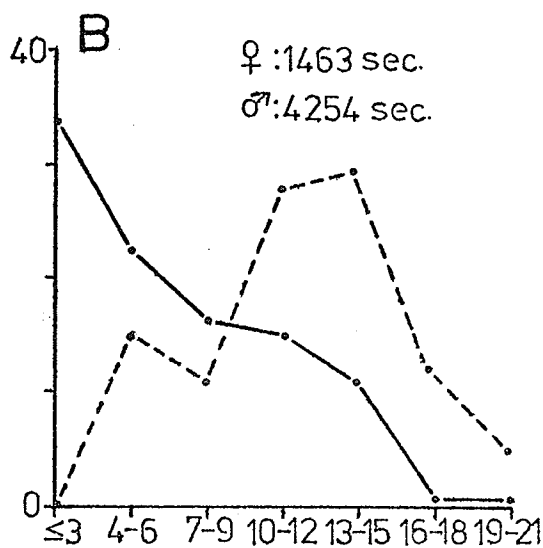A, all periods; B, period I; C, period II; D, period
III; E, period IV.

A
♀ :7467 sec.
♂ :11330 sec.

♀ =
♂ =

% of total secs. of foraging

60

30

0

Ash   Maple   Willow

B
♀ :1039 sec.
♂ :3966 sec.

C
♀ :3784 sec.
♂ :4795 sec.

D
♀ :1865 sec.
♂ :1770 sec.

E
♀ :779 sec.
♂ :799 sec.

80

40

0

A M W   A M W   A M W   A M W
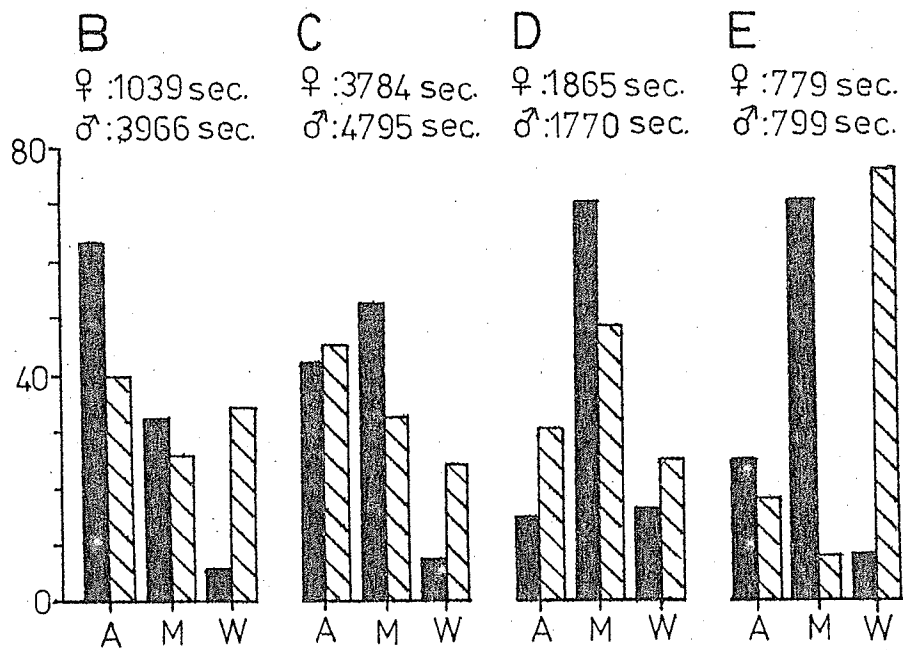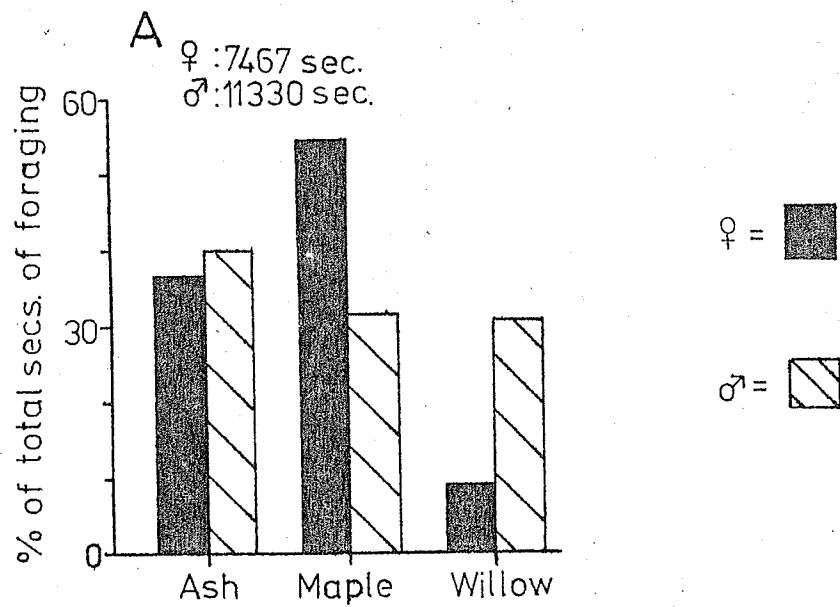
DISCUSSION

Prey Availability

Assessing the availability of prey requires more than
simply measuring the abundance of arthropods in the area
where the predator forages. Behavioral, morphological and
physiological characteristics of certain prey may influence
the predator's rate of predation on them (Tinbergen 1960).

For example, the relatively slow reaction of chironomids
to rapid movements (pers. obs.) may make them easier prey
than other flying insects. The late instars of the forest
tent caterpillar were not taken by Yellow Warblers despite
their great abundance in 1976. Twice I observed Yellow
Warblers attempting to feed on them; the caterpillars
dropped to the ground and were not pursued further. Per-
haps the dense, large spines prevented the birds from
swallowing the caterpillars whole, the usual method for
Yellow Warblers. The larger Black-billed Cuckoo (Coccyzus
erythropthalmus) and the Northern Oriole consumed the
caterpillars and pupae (Oriole) on the ridge (Sealy 1978;
Pers. obs.). The smaller Warbling Vireo traps the insect
between its foot and a branch and tears it apart. Root
(1967) found that Blue-gray Gnatcatchers (Polioptila
caerulia) completely avoided forest tent caterpillars (M.
constricta). Also certain arthropod groups may have an
unpleasant taste and are therefore avoided (Tinbergen 1960,
Sloan and Simmons 1973; but see Royama 1970). Such may be

the case with laydybird beetles (Coccinellidae)(T. Galloway, pers. comm.) which formed a minor but regular component of the arthropods available but were never found in a Yellow Warbler stomach.

In spite of these exceptions, I believe that the arthropod samples were representative of the available food supply (see also De Long 1932, Beall 1935, Whittaker 1952, Lowrie 1971, Janzen 1973). In support of this statement, all insect families found in the stomachs were also found in the sweep net samples. Furthermore, the birds diet closely approximated the composition of the arthropod samples and major changes in the sweep samples were reflected in the stomach contents.

Diet

The arthropod-limited diet of Yellow Warblers during the breeding season along the Delta Beach Ridge is consistent with reports by Kendeigh (1947), Bent (1953) and Frydendall (1967). My study, however, is the only one where Diptera forms the major portion of the diet. Forbes (1883, in Bent 1953) found that Lepidoptera larvae were the most numerous food item; Coleoptera and Arachnida were of lesser importance. Kendeigh (1947) reported the contents of four Yellow Warbler stomachs to consist largely of Homoptera (especially Aphididae) and Coleoptera. Frydendall (1967) found that in 98 Yellow Warbler stomachs taken in Utah, Hymenoptera were the most numerous prey item,

followed by Diptera, Hemiptera and Coleoptera. The present
study indicates that Diptera (especially Chironomidae)
is the dominant group in the diet (66% and 76% in 1975 and
1976, respectively); Lepidoptera larvae (especially Geo-
metridae), Coleoptera, Hemiptera, Homoptera and Hymenop-
tera being of lesser importance.

Yellow Warblers have been reported twice taking non-
arthropod food. Brooks (1933) observed them "picking an
occasional grape" and Stone (1941) saw them feeding on
elderberries in California. Although I found a few pieces
of plant material in stomachs, these probably were accident-
ally ingested while capturing arthropods (see also Root
1967).

Yellow Warblers are apparently flexible in their choice
of food. Prey taken varies in time and space according
to what is available. When the composition of the diet is
analysed by a standard diversity index (MacArthur and
MacArthur 1961), H= - pi ln pi, where H= diversity and pi=
total numbers of the ith prey item divided by the total
number of all prey items, a value of 2.0 was obtained for
Yellow Warblers in this study. Little information is
available on feeding diversity of small insectivorous birds
with which to compare Yellow Warblers. However, from data
presented by Root (1967) a diversity of 2.95 was calculated
for the Blue-gray Gnatcatcher (a diverse and unspecialized
feeder). However this figure includes food items eaten
throughout the year whereas the Yellow Warbler data repres-

ents only the breeding season. Orians (1966) reported that
the feeding diversity of Yellow-headed Blackbirds (Xantho-
cephalus xanthocephalus) varies from 0.06 to 0.39 depend-
ing on the time of day, and Snelling (1968) obtained
figures of 3.17 and 2.62 for Redwinged Blackbirds (Agel-
aius phoeniceus) and Common Grackles (Quiscalus quiscala),
respectively; he concluded that both species were diverse
feeders. However these two figures were based on adults
feeding young; the added stress of feeding young would
probably make the birds less selective in their choice
of prey items thus raising the value. I conclude, then,
that Yellow Warblers along the Delta Beach Ridge are also
diverse and unspecialized arthropod feeders.
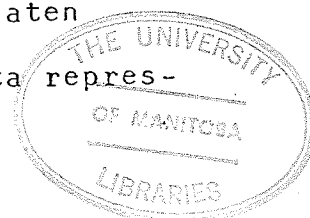
Some evidence from the present study suggests that
Yellow Warblers are opportunistic feeders. A male taken
on 26 May 1975, had consumed 47 scatopsid flies, an insect
not commonly found in the sweep samples. No other warbler
stomach contained these flies. Also, in both years, 10 and
17 prey types, respectively, were found in only one stomach.
This suggests that individuals will exploit certain prey
items which have a very limited spatial or temporal dist-
ribution in the habitat.

Diet versus Prey Availability

Despite the discrepancies between prey taken and prey
available in some of the breeding season periods (espec-
ially period I), the the data from Figs.8a and 9a indicate

that Yellow Warblers on the Delta Beach Ridge take prey
in proportion to its availability. Differences that do
exist may be the result of the birds being selective in
their choice of prey or because the samples were not truly
representative of the diet.

I believe the latter situation to be true. First, stomach
sample sizes for the individual periods were small (bet-
ween nine and 17 depending on the period and year). Since
Yellow Warblers are opportunistic, generalized feeders and
since many insects have a clumped distribution (Borror et al.
1976), it is probable that any given small sample of birds
would not reflect the general arthropod fauna of the area.
A bird preying heavily on a "clump" of arthropods would
cause the diet information to "outweigh" the availability
information. Conversely, a sample of birds missing a
"clump" of a particular prey group would result in the
availability data "outweighing" the diet information.
Second, the availability data and the diet data were coll-
ected on adjacent areas of the ridge. Although occasional
sampling from both areas revealed similar arthropod fauna,
certain changes in the arthropods may not have been ident-
ical in both areas. Third, the pattern of the 1975 and
1976 data is not consistent. For example, during period I
in 1975, chironomids were taken in smaller proportions to
their availability while in 1976 the opposite occurred.
In 1975 (period I) geometrid larvae were taken in propor-
tion to their availability but in 1976 they were taken in

lesser proportions relative to their availability. In 1975, "all other insects" were taken in greater proportions than their availability but in 1976 they were taken in proportion to their availability. Since in both years the birds were at the same stage of breeding and thus having similar requirements, the data should at least be consistent if it were to reflect a true relationship.

Frydendall (1967) concluded that Yellow Warblers in Utah fed randomly on any arthropods of appropriate size. My data are in agreement with his conclusions.

Other warblers also generally take prey in proportion to its availability. Stenger (1958) found that feeding Ovenbirds (Seiurus aurocapillus) in Algonquin Park, Ontario, showed no selectivity for preferred food items and most invertebrates were taken in proportion to their availability. Zach and Falls (1975) observed Ovenbirds that responded functionally to a spruce budworm (Choristoneura fumiferana) outbreak by eating them regularily even though they were located primarily in trees, an unusual foraging site for Ovenbirds. This suggests that this species is opportunistic, and like the Yellow Warbler, can exploit temporarily abundant prey.

McAtee (1932) reported insects occurring in the diet of 80,000 Nearctic birds in approximate proportions to their availability. Kendeigh (1947) and Mitchell (1952) found that most warbler species took all major orders of arboreal arthropods and MacArthur (1958) suggested that any differ-

ences in the diets of five coexisting warbler species studied were best explained in terms of different feeding zones. In the present study, males, which foraged in higher zones, took more geometrid larvae and fewer damselflies and mosquitoes than females, which foraged lower. These data support MacArthur's ideas. Much anecdotal information (Bent 1953) further suggests that parulids are opportunistic feeders and feed primarily on a wide variety of arthropod prey.

Although I did not determine the relative size of prey available and prey eaten, several studies suggest that small insectivorous birds select larger-than-average prey items (Betts 1955, Tinbergen 1960, Gibb and Betts 1963, Royama 1966, Root 1967, Morse 1976). The adaptive value of selecting larger-than-average food items is that, generally, larger prey contains more energy and confers more efficient energy use (Emlen 1973). Willson (1971) and West (1973) found that Tree Sparrows (Spizella arborea) selected smaller-than-average food items, however this was probably due to the relative ease with which the smaller seeds can be husked.

Foraging Behavior

This study indicates that male and female Yellow Warblers on the Delta Beach Ridge behaviorally partition the habitat with respect to their foraging (see also Morse 1973). The relatively high-foraging males may reflect their habit of

foraging in the most conspicuous manner possible, thus
promoting territory establishment and maintenance (Kendeigh
1941, Frydendall 1967, Morse 1968). In the present study,
the difference in the height of males and females is great-
est in the pre-egg stage, the principal period of terri-
tory establishment. The decrease in male foraging height
later in the season probably reflects the time spent
feeding the incubating female (period II) and the nestlings
(period III) at the relatively low nest (Goossen, in prep.).
The relative stability of foraging height of the females
in the first three periods probably reflects their nest-
centered activities. In other studies, females have also
been found to forage closer to the nest height than the
height of the foraging males (Morse 1968, Williamson 1971).
The increase in the foraging height of both males and
females late in the breeding season may reflect their
termination of nest-centered activities and their resump-
tion of self-maintenance behavior and the onset of molt.

Foraging in the upper and outer tree sections promotes
male conspicuousness. Again, the trend is most obvious
in period I, the period requiring the highest degree of
conspicuousness, but persists throughout the breeding
season. Females foraging in lower, less exposed sections,
are less conspicuous and probably better able to attend
to nesting activities with less interference from other
males or other species. The increased foraging height of
females in period IV is probably due to termination of

nesting activities.

The tendency of males to forage in higher trees, a trend which continues throughout the breeding season, may reflect two factors: first, males frequently foraged in large willow trees (17 m or higher). The foliage of these trees is less dense than ashes or maples, and would thus promote male conspicuousness and be detrimental to female conceal-ment. Second, the greater use of shrubs by females would lower the average tree height for them (both trees and shrubs were used in calculating tree heights of foraging birds). Both of these observations are supported by my data; males selected willows more and shrubs less than females.

The species of tree used for foraging was possibly affected by the infestation of forest tent caterpillars on the ridge in 1976. These insects, which primarily attacked ash trees on the study area, increased gradually throughout and peaked in abundance around the end of per-iod I. At this time, most ash trees were entirely defol-iated. The use of ash trees by females sharply decreased in periods II and III, probably as a result of this defol-iation. Males' use of ash trees actually increased in per-iod II. Although Fashingbauer et al. (1957) did not look at sexual differences, they found that defoliation by forest tent caterpillars in Minnesota did not affect densities, territory size, singing perches, nesting sites

or hatching success of several passerine species.

The shift by females to maples during this period of defoliation and the tendency of males to feed in the large willows probably accounts for the statistical differences in the tree species selected by the sexes. Frydendall (1967) found that male Yellow Warblers selected maple trees and river birch (<u>Betula fontenalis</u>) over sierra willows (<u>Salix melanopsis</u>), probably because of the greater abundance of arthropods associated with the preferred trees. In the present study the apparent favoring of maples by females may be partially due to a greater abundance of food, however their avoidance of willows may be related to the relatively sparse foliage. Conversely, males may choose willows more often as the food supply is at least equal to the other tree species but the sparse foliage affords them conspicuousness.

In period I, the long flights of males and females probably reflect their habits of feeding while engaged in territory maintenance (males) and of feeding while collecting nesting materials (females). In period II, the nesting females are less mobile than the males that are still maintaining territories and making frequent feeding trips to the nests. In period III, the females became more active to assist in feeding the young, thus equalling the distances moved by males. The non-significant difference in period IV again probably reflects the end of nest-centered activities. Sexual differences in the distance moved by

foraging birds is also found in Henslow's sparrow (Ammo-spiza henslowii)where males forage farther from the nest than do females (Robbins 1971).

Differential foraging methods of the sexes have been observed in Red-eyed Vireos (V. olivaceus)(Williamson 1971) and several species of Dendroica warblers (Morse 1968, 1971a). Although Yellow Warblers mainly glean, males do so more often and hover less than females. Williamson (1971) discussed her results in terms of the aspect ratio of the wings. Females have a shorter and broader wing (low aspect) than males whose wings are longer and narr-ower (high aspect). Vaughan (1959) concluded that bats with a low aspect ratio were best adapted for hovering and those with a high aspect ratio were better adapted to rapid, prolonged flights. Female Yellow Warblers also have shorter wings than males, which may promote greater efficiency in using hovering manoeuvers.

Females hovered most during the egg-laying, incubation and nestling periods. During these periods the feeding movements of females were extremely rapid and varied. Presumably this maximized the food intake while minimiz-ing the time away from the nest. The percentage of hawk-ing and hovering manoeuvers by males and females decreased sharply in period IV. This is probably related to molt when the birds are least able to perform these movements (see also Frydendall 1967).

GENERAL DISCUSSION

From the foregoing examination of the feeding ecology
of adult Yellow Warblers on the Delta Beach Ridge, it is
evident that 1) the population nests at high densities,
apparently unparalleled elsewhere in its range, 2) there
appears to be an unlimited food supply available to these
and other insectivorous birds throughout the breeding
season, 3) adult midges are the most abundant arthropod
and comprised more than half of the available arthropods,
4) the diets of males and females are very similar through-
out the breeding season and any differences probably
result from different feeding locations rather than diff-
erent prey preferences, 6) the prey taken is restricted
to arthropods and varies spatially and temporally, 7) in
general, Yellow Warblers take prey in proportion to its
availability, and 8) males and females behaviorally part-
ition the habitat with respect to their foraging. Although
the differences are statistically significant, overlap
exists.

The numerical response (Holling 1959) of animals to
unusually high food abundance is well documented (Lack
1946, Kendeigh 1947, Morris et al.1958, Morse 1971b,
Schoener 1971). On the Delta Beach Ridge the response
appears to be to a permanently unlimited food supply,
compared to the usual temporary increase in food found

in other studies; adult midges from over 30 species provide the principal food source.

Generalized, flexible diets are generally favored in temperate climatic regions where food supplies fluctuate both taxonomically and numerically (Morse 1971b, Schoener 1971, Emlen 1973). The present study indicates the highly dynamic nature of the food supply on the Delta Beach Ridge and the adaptive value of the generalized diet of Yellow Warblers there.

The foraging behavior of animals is thought to occur in a manner which maximizes their fitness (Schoener 1971) and achieves optimal profitability (Royama 1970, Smith and Dawkins 1971, Smith and Sweatman 1974, Zach and Falls 1976). It is under the influence of natural selection and subject to certain constraints (Pyke et al. 1977). The underlying assumption that food is limiting (Morse 1971b) provides the mechanism on which natural selection can act. Behavioral (and morphological) foraging adaptations can therefore be viewed as adaptations to reduce competition for a resource (food). Spatial partitioning of foraging location has been discussed as one such adaptation to increase the efficiency of energy use (Morse 1968, Weins 1969, Robbins 1971, Williamson 1971). Generally it is thought that an overall decrease in energy expenditure occurs in a situation of sexual division of the habitat. The males advertising their presence from tree tops and confining their foraging to that area would expend less

energy than those foraging lower and intermittently flying
back to higher singing posts. Similarily, females forag-
ing near the nest would expend less energy than those
making frequent longer trips to and from the nest. The
time and energy saved by increasing foraging efficiency
can be directed into other essential activities such as
nest and territorial maintenance thereby increasing the
probability of reproductive success.

In the present study, the partitioning of the habitat
in spite of the apparently unlimited food supply seems
somewhat paradoxical and contradictory to the theory that
partitioning is a response to a restricted food supply.
However several possible explanations exist. The part-
itioning may be an adaptation to an unpredictable food
supply ensuring that in years of low food abundance the
most efficient use of the available food will be made.
The partitioning may also be under genetic control, evolv-
ing in areas of lower food abundance. Alternatively, the
condition may be unrelated to food supply and may be a
manifestation of the breeding activities of the birds.
For example, the partitioning of male and female Yellow
Warblers may simply represent the "duties" of the sexes,
males feeding in high, conspicuous locations to facilitate
territorial maintenance and females feeding in a more
concealed manner to facilitate nesting success. These
possibilities are not independent of each other and a
combination of the three may be involved. The present

study lends support to the latter possibility but does not refute the others.

Although food seems to play a role in promoting the density of Yellow Warblers on the Delta Beach Ridge, other factors are also known to influence density. Kengeigh (1941), Ficken and Ficken (1965) and Flack (1976) have discussed the importance of high singing posts, concealing cover, suitable nest sites, feeding areas in trees and some open space. It appears that both food supply and habitat characteristics are important in determining the density of Yellow Warblers on the Delta Beach Ridge.

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Appendix I. Summary of diet information of Yellow Warblers for 1975 and 1976. Numbers in parenthesis are sample sizes.

1975	Period I ♂(5)	♀(4)	T(9)	Period II ♂(6)	♀(8)	T(14)	Period III ♂(8)	♀(6)	T(14)	Period IV ♂(6)	♀(4)	T(17)	Combined periods I-IV ♂(25)	♀(22)	T(54)
Diptera															
Chironomidae	36	49	85	42	154	196	73	71	144	59	23	82	210	297	507
Anthomyiidae	7	9	16					1	1				7	10	17
Phoridae	4	11	15										4	11	15
Syrphidae	2	1	3										2	1	3
Empididae	1	3	4										1	3	4
Tabanidae	1		1		2	2							1	2	3
Tachnidae	2		2										2		2
Sphaeroceridae	1		1										1		1
Tipulidae	1		1										1		1
Culicidae	2		2										2		2
Sciomyzidae				1		1	3		3				4		4
Ceratopogonidae				1		1							1		1
Unident.	2		2					1	1				2	1	3
Pupae															
Hemiptera															
Miridae	2	1	3	2	1	3	1	9	10				5	11	16
Tingidae	2	3	5	1		1							3	3	6
Corixidae		1												1	1
Nymph					1	1	6	1	7				6	2	8
Homoptera															
Psyllidae	2	2	4								12	12	2	14	16
Membracdae					1	1	1		1				1	1	2
Aphididae										1	3	4	1	3	4
Cicadellidae											1	1		1	1
Coleoptera															
Chrysomelidae	12	15	27	1	1	2	1	1	2	23		23	37	17	54
Anobiidae	6	5	11	5	1	6	1	1	2				12	7	19
Stapnylinidae		1	1											1	1
Unident. #1		6	6							7	1	8	7	7	14
Cantharidae					4	4		2	2					6	6
Curculionidae										1	1	2	1	1	2
Unident.		2	2	2	1	3	2	3	5	1	1	2	5	7	12
Hymenoptera															
Pteromalidae	1	1	2	4	1	5	1		1		1	1	6	3	9
Ichneumonidae	1		1				1	1	2	1	7	8	3	8	11
Platygasteridae		1	1	2		2							2	1	3
Cynipidae							1		1	1		1	2		2
Lepidoptera															
Geometridae (lar.)	5	1	6	47	20	67	9	5	14	3	4	7	64	30	94
Unident.Ad.								1	1	2	1	3	2	2	4
Larvae (unident.)											6	6		6	6
Odonata															
Coenagrionidae								4	4					4	4
Nymph							1		1				1		1
Trichoptera															
Leptoceridae										2	1	3	2	1	3
Limnephilidae										1		1	1		1
Arachnida	1	2	3		1	1		2	2		1	1	1	6	7

Appendix 1 cont'd

1976	Period I			Period II			Period III			Period IV			Combined periods I-IV		
	♂(5)	♀(4)	T(9)	♂(7)	♀(8)	T(15)	♂(5)	♀(6)	T(11)	♂(3)	♀(2)	T(5)	♂(20)	♀(20)	T(40)
Diptera															
Chironomidae	51	58	109	12	142	154	36	56	92	29	18	47	128	274	402
Tipulidae		2	2											2	2
Scatopsidae	47		47										47		47
Simuliidae		5	5											5	5
Empididae	4	3	7	7	7	14		3	3				11	13	24
Culicidae		20	20	2	3	5							2	23	25
Sciomyzidae		1	1											1	1
Ceratopogonidae		2	2		1	1								3	3
Muscidae	1	2	3	2	1	3							3	3	6
Chloropidae		1	1											1	1
Dolichopodidae		.		3	2	5	1	1	2				4	3	7
Anthomyiidae	5			5	1	6		4	4	5		5	10	5	15
Tachnidae					2	2		2	2					4	4
Stratiomyidae					1	1								1	1
Syrphidae					2	2								2	2
Drosophilidae					1	1								1	1
Sciaridae							1		1				1		1
Agromyzidae										1		1	1		1
Hemiptera															
Miridae	2		2		1	1		1	1				2	2	4
Homoptera															
Aphididae					1	1	6		6		2	2	6	3	9
Cicadillidae					3	3								3	3
Coleoptera															
Chrysomelidae	11	5	16				1	1	2				12	6	18
Unident. #1	2		2										2		2
Anobiidae					4	4		1	1					5	5
Cerambycidae					1	1								1	1
Cantharidae					1	1	1		1				1	1	2
Curculionidae														1	1
Unident.	1	1	2										1		1
Hymenoptera															
Platygasteridae		1	1											1	1
Ichneumonidae	1	5	6		2	2				1		1	2	7	9
Pteromalidae	2		2	3	2	5		3	3				5	5	10
Tenthredinidae		1	1		1	1							2	2	4
Braconidae							2	2	4				2	2	4
Larvae (Unident.)										1		1	1		1
Lepidoptera															
Lasiocampidae (lar.)	1	2	3		1	1							1	3	4
Geometridae (lar.)	3	5	8	30	8	38	1		1				1		1
Lasiocampidae (ad.)					1	1							1		1
Trichoptera															
Limnephilidae					1	1								1	1
Leptoceridae				3		3	1	5	6				4	5	9
Odonata															
Coenagrionidae				2	5	7	1	3	4				3	8	11
Plectopera															
Chloroperlidae				1	1	2							1	1	2
Neuroptera															
Chrysopidae															
Psocoptera															
Psocidae							3		3				3		3
Arachnida		5	5		5	5	4	1	5				4	11	15