

## FEEDING RATES OF WARBLERS IN SPRING

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**ABSTRACT.**—Populations of migrant warblers were correlated with populations of lepidopterous larvae in spring in a heavily forested area of southern Illinois. The birds appeared to feed entirely on these larvae, mostly taken from oaks. Estimates of gross calorie intake indicated a positive energy balance for warblers in an area with larval biomass of 0.70 g per m<sup>3</sup>, and a negative balance in an area with biomass of 0.02 g per m<sup>3</sup>. Warblers chose either the smaller size classes (under 15 mm) of larvae, or the smaller species (especially leafrollers) out of proportion to their availability, but the birds' positive energy balance was dependent upon an irruption of geometrids. Lepidopterous larvae constituted 75–98% of the available foliage invertebrates, and other groups were insufficient alone to support migrant populations. Larvae were about 80% water, and warblers ingested 1.2–1.7 times their own weight in larvae per day in order to attain gross caloric intake of 14.8–19.0 kcal per bird-day. Warblers in an area with insufficient food resources ingested 7.2 kcal/day, and their behavior was consistent with a goal of energy conservation.

Among the problems faced by migrants after a flight is that of finding adequate food supplies to continue the migration, particularly as the landing area may be completely unknown to the birds. In Illinois the only measurements of migrant populations in forest habitat have been those of Twomey (1945) and Calef (1953) who found four to eight times more birds in elm-maple forest at the peak of migration in May than were present in June. We wondered how the forest accommodated large numbers of migrants, and how much forest is required by arboreal migrants. Kendeigh's (1979) study of invertebrates in three east-central Illinois study areas showed the seasonal population patterns of various groups of invertebrates. There was a close similarity between the timing of emergence of lepidopterous larvae and the seasonal timing of bird migration in this region.

Stimulated by these papers and the question of how migrant populations respond to habitat availability, we began, in 1979, concurrent studies of bird populations and their potential food resources in (1) an area where forest tracts were extensive, and (2) an area where forest was much more restricted. Our primary goal was to consider the availability of food supplies to migrant warblers. Our interest was not in the influence of bird populations on insect populations, but the reverse. In either case, it is important to know about rates of predation. When the opportunity arose in May 1981 to study food consumption by warblers on invertebrates in forest-edge habitat at two widely divergent population levels, we interrupted our

principal study to make the observations reported here.

### STUDY AREAS

Our study area with extensive forest habitat was in Shawnee National Forest in southern Illinois (88°30'W, 37°28'N): mature upland oak-hickory, and upland forest edge in Pope County (57.2% forested). Our study area with more restricted forest was in Allerton Park in east-central Illinois (88°38'W, 40°00'N): mature upland oak-hickory and upland forest-edge in Piatt County (1.8% forested). Figures for forest acreage in each county are from Essex and Gansner (1965). Our original study involved three arboreal habitats in each region, but we restricted our observations on feeding warblers to forest-edge and shrub habitat so that birds would be as low as possible for viewing. Unless otherwise stated, the data in this paper refer to forest-edge and shrub. However, the larger general study was important to this one because of the extensive experience it provided as background to the observations on feeding.

### METHODS

For censusing birds we used the same fixed-width transect method we have used on breeding and winter populations (Grabber and Grabber 1963, Grabber et al. 1977), i.e., counts of all birds detected within a strip of habitat 27.4 m wide and not less than 6.4 km long. In this study the bird census transects were along marked routes, and encompassed 18.7 ha

(Pope) and 19.9 ha (Piatt). The census routes were roughly rectangular, ending near the starting point. We did not census on days with rain and/or sustained high wind (above 15 knots) in the habitat. Bird censuses were conducted in the morning; invertebrate censuses were conducted in the afternoon usually on the same day and in the same habitat as the bird census. With the techniques used we could not census birds and invertebrates at the same time. Lepidopterous larvae, which constituted 75–98% of the foliage invertebrate biomass, are not very mobile and are generally present in the same feeding area day and night during the period of their development. For several groups of larvae we checked their location and numbers at different times over a period of two weeks or more and found them consistently in the same sites.

The invertebrate censuses were counts of individuals of all species detected (excluding galls) on or flying through the woody vegetation in a cubic meter (measured with a meter stick) 1–2 m above ground level. Samples ( $m^3$ ) were spaced evenly at intervals of 32 m along the middle of the bird census transect. The interval was measured by pacing 20 (left foot of RRG) paces. The point of the toe on the twentieth pace indicated which plant would be censused, i.e., from that point the nearest woody plant at least 2 m tall. As the starting point of the census was randomly selected ( $n$  paces along the transect line), selection of plants was random, and reflected shrub and tree species at least roughly proportional to their numbers along the transect. One afternoon's invertebrate census covered only about one-seventh of the entire bird census route and subsequent invertebrate censuses were taken on different sections of the over-all route. After the first 20 samples were censused each day, we modified the selection procedure to examine dominant species that had not been covered that day—selecting plants close to, but not necessarily closest to, the point. This gave us more complete coverage of the dominant plant species, and spread the sampling evenly along the transect line. The counts and measurements of invertebrates were made by JWG, and were recorded by RRG. Some quadrats 5–7 m high were also censused for invertebrates. Censuses for arboreal invertebrates in forest-edge and shrub, and adjacent forest interior were made on 14 and 24 April, 1, 2, 13, 15, 22, 31 May, 19 June in central Illinois, and on 8, 17, 18, 19, 28 April, 5, 6, 8, 17, 19, 25, 28 May, 14 June in southern Illinois. We censused 23–34  $m^3$  per day in spring 1981.

We began to learn the common foliage invertebrates in 1979 by photographing and col-

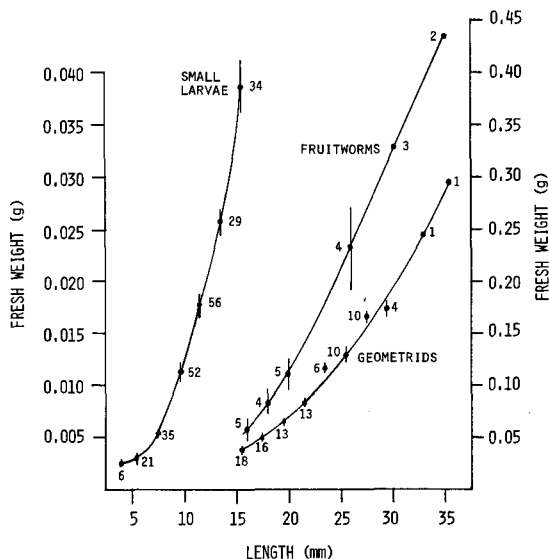


FIGURE 1. Relationship of length to weight in common types of lepidopterous larvae found in forest-edge and shrub habitat in southern and central Illinois study areas. Scale on left refers to curve for small (4–15 mm) larvae of species of leafrollers (Tortricidae), loopers (Geometridae), and fruitworms (Noctuidae, excluding *Amphipyra*). Scale on right refers to larger larvae (15 mm +) of geometrids and fruitworms. Most leafrollers were less than 15 mm. The number of specimens weighed and measured is given beside the appropriate point on the curve. Vertical line indicates  $\pm 1$  SE for each sample.

lecting them. Our colleagues in the Illinois Natural History Survey Section of Faunistic Surveys and Insect Identifications provided identifications of many species, genera, and families. The immature forms especially, of many species of invertebrates are unknown, and so we assigned descriptive code names to all forms that we encountered. Censuses were conducted at first with the aid of a 2 $\times$  hand lens, and later with a 2.5 $\times$  Optivisor magnifier. In addition to counting the invertebrates, we measured in situ (to nearest mm) all individuals found. Sizes of flying insects were estimated. We also weighed specimens (to nearest 0.0001 g) of nearly all the common species and constructed weight-length curves (e.g., Fig. 1) for the different species or different types where the species was unknown to us (e.g., ants). Collected specimens were taken from the same habitats we censused, but not, with very few exceptions, from the census transects. We also collected specimens of the common larvae for dry-weight and caloric determinations (Table 1). Caloric determinations were made with a Parr bomb calorimeter on 1-g (dry weight) samples of caterpillars and sawfly larvae. Tomato hornworms are not arboreal species, but were included in Table 1 to show caloric values in large larvae, and also to show variation in replication of caloric determinations. Speci-

TABLE 1. Caloric values of lepidopterous larvae and sawfly larvae of various species and sizes.

Sample	Larval length (mm)	Number of larvae in sample	Fresh wt. of sample (g)	Percent dry matter	Calories/g dry wt.	Calories/g ash-free dry wt.
Leafrollers ( <i>Archips</i> sp., <i>Argyrotaenia</i> sp.)	10	351	4.9845	19.22	5,930	6,225
Linden loopers ( <i>Erannis tiliaria</i> )	20–25	47	5.1780	19.58	5,401	5,692
Various geometrids ( <i>Alsophila</i> , <i>Paleocrita</i> , <i>Erannis</i> , and others)	10–25	136	6.6557	18.79	5,308	5,567
Mixed caterpillars—leafrollers, geometrids, fruitworms ( <i>Orthosia</i> ), webworms ( <i>Atteva</i> )	7–40	55	5.4485	19.29	5,592	6,157
Uglynest caterpillar ( <i>Archips cerasivorana</i> )	6–25	62	6.8391	18.63	5,460	6,007
Tomato hornworm ( <i>Manduca quinquemaculata</i> )	65	0.5	—	—	4,807	5,181
Tomato hornworm	65	0.5	—	—	5,344	5,795
Tomato hornworm—heavily parasitized with braconid wasps	55	0.5	—	—	4,779	5,073
Tomato hornworm—heavily parasitized	55	0.5	—	—	4,728	5,015
Pine sawfly ( <i>Neodiprion taedae</i> )	13–20	51	5.5665	19.78	4,892	5,304
Larch sawfly ( <i>Pristiphora erichsonii</i> )	13–19	60	5.2578	22.80	5,334	5,808

mens were weighed live, most within one-half hour of being removed from the vegetation. Those saved for caloric determinations were killed by freezing and dried to constant weight in an oven at 90°C.

Our calculations of daily caloric intake by warblers involved three conversions: prey length to prey weight, live weight to dry weight, and dry weight to calories. To simplify the procedure we used one calorie figure—5,666 calories per g dry weight. That figure was derived from calorie data on the different groups of larvae (Table 1) weighted by using (as a multiplier) the percent of food each group comprised of total warbler food. Although caloric values are often presented as calories per g ash-free dry weight, our conversion figure includes the ash weight, as it is part of the larval weight consumed by the birds.

Warbler weights in this paper are average weights of May birds from Clench and Leberman (1978), and the weights for "all warblers" the average for the particular species observed proportional to the time each was observed.

Trees and shrubs of the forest areas had been censused earlier (Graber et al. 1977), but a special census was made of species of trees and shrubs in the forest edge areas where we observed feeding rates. Scientific names of plants are given in the tables. Nomenclature for insects follows Sutherland (1978), except for the fruitworm, *Orthosia* (not listed).

Because of the problem of keeping track of individual birds in large trees, we elected to study feeding rates of migrants in forest edge habitat, where the trees were smaller (average height: 4.8 m in the central area, 5.9 m in the south) and the birds more nearly on our level. With a stop watch (Heuer Microsplit, accuracy: 0.1 s/h) in hand, we walked slowly along the transect line of the forest-edge census area.

One of us (JWG) was primarily responsible for making the observations, while RRG kept the time and recorded the observations as they were dictated. The timer was started the instant a warbler came into good view and stopped the instant it was lost to view. We recorded the species and sex of bird; the number, kind, and size (to nearest 5 mm) of items eaten in the period; the starting time of the observation; and the species of tree(s) or shrub(s) the bird visited during the period. If the bird was obviously resting or preening rather than foraging, we noted the length of the rest period. During prolonged observations, we alternated duties to relieve strain. Most of our observations refer to three warblers, Tennessee (*Vermivora peregrina*), Blackpoll (*Dendroica striata*) and Palm (*D. palmarum*), but we made foraging observations on any warblers that came into good view—i.e., Black-and-white (*Mniotilta varia*), Golden-winged (*Vermivora chrysoptera*), Blue-winged (*V. pinus*), Nashville (*V. ruficapilla*), Magnolia (*Dendroica magnolia*), Yellow-rumped (*D. coronata*), Black-throated Green (*D. virens*), Blackburnian (*D. fusca*), Chestnut-sided (*D. pensylvanica*), Bay-breasted (*D. castanea*), Prairie (*D. discolor*), Common Yellowthroat (*Geothlypis trichas*), and American Redstart (*Setophaga ruticilla*). Reference in this paper to "all warblers" refers to our combined data on all these species. It was imperative that the bird be seen clearly, thus the potential number of observations was much greater than the actual number. In the southern area defoliation was extensive, making observation much easier than in the central area, where there was no obvious defoliation. Identification of food items was facilitated by our familiarity with foliage invertebrates from the daily censuses, 1979–1981. We also knew the

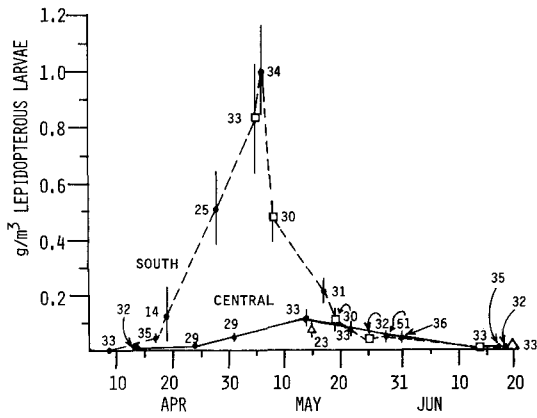


FIGURE 2. Variation in seasonal abundance of lepidopterous larvae in upland forest (solid dots) and adjacent forest-edge and shrub habitat (open squares and triangles) in southern and central Illinois in 1981. Numbers show sample size for each date. Vertical line indicates  $\pm 1$  SE for the sample.

frequency of size classes in each species. We tested our ability to differentiate size classes of larvae in a controlled experiment. From a distance of 10.5 m the principal observer (JWG), in 16 tests, differentiated 5-mm size classes in a range of 5–40 mm without error. The second observer (RRG), in 16 tests, made two errors, each of 5 mm. The tests were made with cut pieces of rubber band of uniform color to test size differentiation, vs. species differentiation. Species differentiation is easier because of the clues of color, pattern, shape and habit (e.g., leafrollers in characteristic leaf rolls). Our skill

at estimating size in controlled tests was undoubtedly related to three years of experience measuring thousands of larvae. Most of the feeding observations were made within a 10-m distance to the bird and none exceeded 15 m. There was not time to measure observation distance during the feeding observations, but the longer-range observations were marked, and measured after the feeding observations were completed.

Observations on feeding rates were made 3–8 May in the south, and 12–16 May in the central area, when bird populations and insect populations were relatively high (Figs. 2, 3) in order to obtain the most observations in the time available. Both populations changed fairly rapidly from day to day, and so we had only a few days on which to make feeding observations, and still continue the censuses.

## RESULTS

### FOOD RESOURCES AND FORAGING BEHAVIOR

For arboreal foliage-gleaning birds, the dominant potential food on our study areas in spring was lepidopterous larvae (Table 2). These constituted 75–98% of the invertebrate biomass in spring in different areas. Furthermore, the only food items of warblers we actually identified in spring were larvae. Sawfly larvae, which superficially resemble caterpillars, and which are eaten by birds, constituted only 0.004%, or less, of the total biomass. Groups other than Lepidoptera had their peak populations in late summer or fall.

TABLE 2. Numbers and biomass of lepidopterous larvae and other invertebrates on forest foliage in southern (S) and central (C) Illinois, 5–15 May 1981.

Specimens	Area	Upland forest		Forest edge	
		$n/m^2$	$g/m^2$	$n/m^2$	$g/m^2$
Leafrollers (Tortricidae, and possibly other groups, all unidentified species)	C	2.4545	0.0279	1.8148	0.0177
	S	0.6471	0.0229	1.1167	0.0206
Linden loopers ( <i>Erannis tiliaria</i> )	C	0.0303	0.0003	0	0
	S	5.8529	0.8616	3.4333	0.4964
Other geometrids ( <i>Paleocrita</i> , <i>Alsophila</i> , <i>Ennomos</i> , <i>Lambdina</i> , and others)	C	0	0	0.0555	0.0006
	S	1.1176	0.1019	1.1333	0.0994
Fruitworms (mainly <i>Orthosia</i> , <i>Lithophane</i> , <i>Hiemella</i> , <i>Amphipyra</i> , <i>Eupsilia</i> )	C	0.2121	0.0294	0.0555	0.0034
	S	0.3529	0.0702	0.1333	0.0223
Other larvae ( <i>Catocola</i> , <i>Malacosoma</i> , <i>Haploa</i> , <i>Archips</i> , <i>Papilio</i> , <i>Graphium</i> , <i>Coleophora</i> , <i>Yponomeuta</i> , <i>Alypia</i> , sphingids, thyatirids, and many others)	C	0	0	0.0926	0.0002
	S	0.3823	0.0635	0.5167	0.0624
Total lepidopterous larvae	C	2.6969	0.0576	2.0185	0.0219
	S	8.3529	1.1201	6.3333	0.7011
Other invertebrates	C	1.9410	0.0074	1.8305	0.0071
	S	0.5880	0.0162	2.2180	0.0351
Percent of total = Lepidoptera larvae	C	58.15	88.61	52.44	75.52
	S	93.42	98.57	74.06	95.23

TABLE 3. Numbers and biomass of lepidopterous larvae and other invertebrates on foliage at heights of 1–2 m and 5–7 m in upland forest in southern Illinois.

Date	Ht (m)	Number of quadrats	Lepidopterous larvae		Other invertebrates	
			n per m <sup>3</sup>	g per m <sup>3</sup>	n per m <sup>3</sup>	g per m <sup>3</sup>
17 April	1–2	35	6.97	0.048	1.66	0.019
18 April	5–7	14	7.43	0.076	1.29	0.095
28 May	1–2	26	0.42	0.130	3.65	0.038
28 May	5–7	25	0.64	0.202	2.68	0.044

The invertebrate populations of the high canopy in our study areas were unknown. Our observations were made of birds foraging at heights under 6 m. Comparative censuses of invertebrates at heights of 1–2 m and 5–7 m showed the same general pattern of change between two dates (Table 3). At high larval densities (above 0.3 g per m<sup>3</sup>) defoliation appeared to be uniform from the understory to the top of the canopy.

The invertebrate population on arboreal foliage changed daily, some species entering and others leaving the population. The populations

also varied from one plant species to another, so statistics on variation should relate to specific dates and specific plant species. The time we had to census invertebrates (4–6 h per day), and the number of plant species censused precluded large samples from a particular plant species on a specific date and the variation shown in Figure 3 includes all the plant species censused on a given date.

The spring arrival of warblers in southern Illinois coincided with irruptions of lepidopterous larvae in 1979, 1980 (Graber and Graber 1980) and 1981, with peak numbers of warblers present in arboreal habitats at or near the peak of the larval population (Fig. 3). Warblers reached central Illinois generally before the larval population peaked. Larval populations were consistently higher (and warbler population densities lower) in the heavily forested south than in central Illinois. Populations of larvae in southern Illinois were at a very high level from 1979 to 1981. In 1981 defoliation by geometrids was extreme and extensive south of latitude 39°N in Illinois. In contrast, east-central Illinois north of that latitude had very low larval populations, provid-

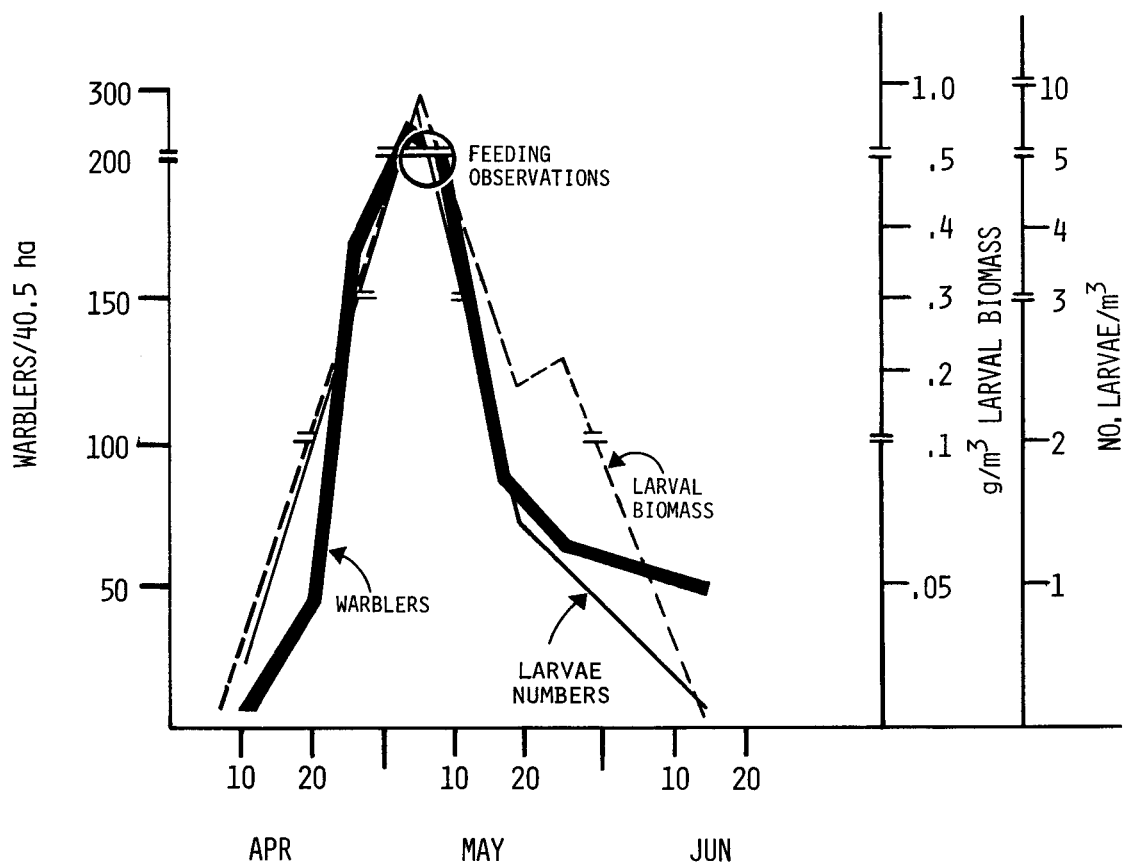


FIGURE 3. The abundance of lepidopterous larvae correlated ( $r = 0.947$ ,  $P = <0.01$ ) with the numbers of spring warblers in upland forest, and forest-edge and shrub habitats in southern Illinois in 1981. Observations on foraging (indicated by circle) were made near the peaks of abundance of both larvae and warblers.

TABLE 4. Feeding rates and calorie intake of warblers on two study areas with different prey populations.

Species and area	Average bird wt. (g)	Observ. time (min)	Grams eaten per min	Percent of time foraging	Food* intake—g per day (wet wt.)	Average** feeding period (min)	Average rest period (min)	Correc-tion factor for feeding time	Corrected calcula-tion/food intake per day (wet wt.)	kcal/bird-day
South										
All warblers	11.1	283.07	.0374	66.5	24.72	7.39	8.94	.68	16.82	19.05
Tennessee Warbler	10.0	48.13	.0257	45.0	17.76	6.06	8.38	.93	16.56	18.77
Blackpoll Warbler	12.6	96.78	.0384	54.0	21.26	7.38	11.04	.74	15.77	17.87
Palm Warbler	10.2	83.79	.0511	68.2	16.63	9.31	8.01	.62	13.10	14.85
Central										
All warblers	9.9	76.71	.0126	98.0	5.49	7.39	1.37	.86	6.37	7.23

\* Based on observed foraging time (Fig. 4).

\*\* Based on the longest observation periods.

ing circumstances for comparative study of foraging behavior of migrants at two levels of food resources.

The advantages of an abundant food supply to migrant warblers were apparent in the general behavior of the birds. In the south, warblers could be approached and watched relatively easily as they foraged leisurely from branch to branch. They did not move far even when they flew. By contrast, warblers in the central area appeared wild, moving almost constantly. In the south, warblers typically ate from 1 to 17 larvae (one at a time) in a period of 1 to 16 min, then rested from 1 to 13 min. Average feeding period was the same in both regions, but average rest period (excluding the long midday rest) was much longer for all warblers in the south than for those in the central area (Table 4). Resting birds did not sleep or even close their eyes, but sat quietly, or sometimes preened or sang, until the next feeding period. In central Illinois we saw warblers resting only three times. Mainly they were moving from tree to tree searching intensively for food.

So far as we could tell, warblers ate nearly all of the common species of larvae present. We saw only one warbler (a Yellow-rumped) pick up a larva and then discard it as if it were distasteful. All other larvae were swallowed

whole and probably alive with almost no preparation and essentially no lost time. All the larvae that we saw warblers eating were "naked" (not covered with setae or spines), and virtually all the spring larvae on forest foliage were "naked." Notable exceptions were the tent caterpillars (*Malacosoma*) which comprised a very small part of the larval biomass. The largest larva eaten (by a Blackpoll) was a 40-mm geometrid and the bird spent a few seconds subduing it, then ate it whole, without apparent difficulty. We could not tell how many larvae were rejected visually by birds.

Warblers selected either smaller-sized larvae (under 15 mm) or species that were small (notably leafrollers out of proportion to their occurrence on the foliage (Table 5). Only a few of the larvae were taken close enough to be identified specifically. Our designation of larvae as "leafrollers" (Tables 1 and 2) probably includes several species, all unknown to us. Craighead (1950) listed a number of species in this category, and the name does not imply a particular taxonomic group. These larvae have in common the behavior of rolling the leaf edge or tip into a cylinder in which they are concealed much of the time. Our designation does not include the felt larva (*Euthyatira pudens*), which made "peapod" structures of the leaf.

TABLE 5. Size (length in mm) of prey taken by warblers compared to size of prey on arboreal foliage.

	Size of prey (mm)							Total n
	5	10	15	20	25	30	40	
Central study area								
Percent of total taken by warblers	72.6	21.0	2.1	3.2	1.0			95
Percent of total on foliage	64.5	29.1	2.7	3.6				110
	$\chi^2 = 6.14, P = >0.10$							
Southern study area								
Percent of total taken by warblers	34.5	25.7	10.2	5.3	20.9	2.9	0.5	206
Percent of total on foliage	2.4	18.7	7.4	17.5	35.0	18.7	0.3	326
	$\chi^2 = 629.47, P = >0.001$							

Leafrollers were generally small (under 15 mm). Warblers lost little time in removing larvae from leaf rolls, though sometimes Tennessee Warblers—a species that appeared to specialize on leafrollers—had to probe both ends of a roll before extracting a larva. Leaf rolls appeared to be ineffective as defense against Tennessee Warblers especially, and may have even called attention to the prey, as leaf rolls were relatively conspicuous in the foliage. In the area where we made feeding observations, nearly all leaf rolls were of a simple (leaf tip) type. Some leafrollers construct more complex leaf roll structures that may afford greater protection from warblers. The birds we watched did not encounter such structures. Leafrollers constituted 19% of larval numbers in our quadrats, but 57% of the prey taken by warblers in general, and 93% of the Tennessee Warbler's prey. Other species of invertebrates, including other larvae sometimes take refuge in the leaf rolls, but we did not count items taken from leaf rolls as leafrollers unless we actually identified them.

The majority of larvae available (49% of the total  $n$ ) were linden loopers. Only in the very closest observations could we distinguish such insects from similar yellow geometrids. In those cases linden loopers made up 26% of the warbler prey (42% of the *Dendroica* prey). All geometrids combined constituted 65% of the larvae on foliage, but only 42% of all warbler prey (62% of the *Dendroica* prey).

#### PLANTS USED BY WARBLERS

Shingle oaks supplied the substrate for most of the food for warblers foraging in the forest edge (Tables 6 and 7). These trees were dominant plants in the habitat, but not the most abundant species. Shingle oak also supported a high population of larvae, but not the highest biomass of larvae in the habitat. Sassafras, the most frequent woody plant in the forest edge (28% of total) provided only 5% of the food for warblers. Black cherry had the highest biomass of larvae in the habitat but provided only 1% of the warblers' food in the south. Black cherry contains a cyanogenic material (Evers and Link 1972) but whether the compound is transferred to larvae that feed on cherry leaves and subsequently as a toxin to predators is unknown to us. Some unpalatable Lepidoptera contain cyanogenic glycosides that have been incorporated into their larval tissues from food plants (Brower and Brower 1964). However, in central Illinois where food was scarce, warblers took 12% of their food from cherry trees (Table 7).

Shingle oaks may have attracted foraging warblers because of the relatively high popu-

lations of leafrollers that these trees support; 64–82% of all leafrollers counted were on this plant. Oaks, in general, supplied 60% of the food for warblers and 90% of the food for the Tennessee, the most numerous of the migrant warblers in May. Oaks were also very important as foraging sites for Blackpoll and Palm warblers. Palm Warblers relied about equally on oaks and hickories. Blackpoll Warblers utilized a wider variety of plant species than did either the Tennessee or Palm warblers. Elms in the south had very high populations of geometrid larvae in April and were largely defoliated when our observations on foraging were made, thus offering little to attract either larvae or warblers.

At the time our observations were made, many larvae were leaving their initial host plants either because defoliation was complete or because of their state of development. That exodus probably accounts for the occurrence of larvae on ash, red cedar, and sumac, which usually had few or no larvae. Some plants were very heavily infested (e.g., ironwood) but occurred infrequently in the forest edge, and were not observed to be foraging sites for warblers. Flowering dogwood had a relatively large percentage of larval biomass because of the presence of large thyatirid larvae. We did not see any warblers or other birds attempt to eat these larvae. Some species of plants (e.g., honey locust, sycamore) occurred infrequently and were not chanced upon in our random sampling, hence we have no measurements of larval biomass on them (Tables 6 and 7).

#### FORAGING RATES DURING THE DAY

In the south, where prey was abundant, all warblers observed alternately fed and rested throughout the morning. Our observations began at 05:00 before full daylight, and we found warblers foraging by 05:10. Feeding rate increased between 11:00 and 12:00 (Fig. 4), just preceding a prolonged rest period. Although we continued to search we saw only eight warblers between 12:45 and 15:15. We saw them only briefly, but they were not obviously foraging. Warblers in general had either left the area, or had made themselves so inconspicuous that we could not find them. By 15:25 warblers were conspicuous again, foraging at about the same rate as in early morning. The rate increased as darkness approached, and the last birds observed were Palm Warblers, still taking food at 17:55, when it was too dark for us to see what they were taking. Feeding rates increased before a period of fasting both midday and night (Fig. 4). In central Illinois, where food was scarce, foraging was apparently terminated earlier in the morning (Fig. 4). The

TABLE 6. Use of arboreal plants by warblers during spring migration in a southern Illinois area. (Listed in order of percentage of the warblers' food taken from the plant.)

Arboreal species	% Frequency of plant	% Larval biomass	All warblers observed		Tennessee Warbler		Blackpoll Warbler		Palm Warbler	
			% Food	% Time	% Food	% Time	% Food	% Time	% Food	% Time
Shingle oak ( <i>Quercus imbricaria</i> )	13.90	9.30	46.66	41.35	77.16	59.91	50.13	58.11	45.22	29.26
All other oaks* ( <i>Quercus</i> spp.)	6.95	7.85	13.13	9.92	12.73	10.41	20.55	7.19	5.05	10.74
Hickories (chiefly <i>Carya glabra</i> )	3.12	4.08	19.19	14.00	10.03	25.31	0.38	2.33	44.68	30.99
Sassafras ( <i>Sassafras albidum</i> )	27.59	7.89	5.57	14.30			4.55	10.20	5.00	26.65
Honey locust ( <i>Gleditsia triacanthos</i> )	0.38		4.95	0.99	0.08	2.56	14.00	1.55		
Hackberry ( <i>Celtis occidentalis</i> )	1.56	1.08	3.55	3.41						
Elm (chiefly <i>Ulmus alata</i> )	6.30	3.31	2.24	4.72			0	3.13		
White ash ( <i>Fraxinus americana</i> )	4.63	0.81	1.28	2.46			3.61	7.00		
Redbud ( <i>Cercis canadensis</i> )	0.75		1.28	2.46			3.61	7.00		
Black cherry ( <i>Prunus serotina</i> )	5.87	13.23	1.09	1.53	0	1.81	3.10	2.59	0	0.67
Maples ( <i>Acer rubrum</i> , <i>A. saccharum</i> , and <i>A. saccharinum</i> )	2.48	13.49	0.92	1.79						
Sumac ( <i>Rhus copallina</i> and <i>R. glabra</i> )	3.93	1.12	0.03	1.35						
Multiflora rose ( <i>Rosa multiflora</i> )	0.16		0.03	0.50						
Flowering dogwood ( <i>Cornus florida</i> )	1.78	7.95	0.02	0.48					0.05	1.70
Wild grape ( <i>Vitis</i> sp.)	1.72	5.72	0.02	0.12			0.05	0.34		
Sycamore ( <i>Platanus occidentalis</i> )	0.32		0.02	0.07						
Eastern red cedar ( <i>Juniperus virginianus</i> )	2.37	3.27	0	0.35						
Persimmon ( <i>Diospyros virginiana</i> )	1.29	0.19								
Ironwood ( <i>Ostrya virginiana</i> )	1.45	17.53								
Sour gum ( <i>Nyssa sylvatica</i> )	0.65	1.50								
Japanese honeysuckle ( <i>Lonicera japonica</i> )	8.73	1.68								
All other arboreal species**	1.92									
Dead stubs	2.21		0	0.21	0	0	0	0.58	0	0
Total number of plants = 1,856										

\* Other oaks include post oak (*Q. stellata*), red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), and chinquapin oak (*Q. muhlenbergii*).

\*\* Includes cottonwood (*Populus deltoides*), mulberry (*Morus rubra*), walnut (*Juglans nigra*), black willow (*Salix nigra*), poison ivy (*Rhus toxicodendron*), green brier (*Smilax* sp.), trumpet creeper (*Campsis radicans*), and woodbine (*Parthenocissus quinquefolia*).

birds searched vigorously until 10:00, after which we could find very few warblers; they resumed feeding at about 16:00, when they fed at a rate higher than we noted in the morning.

Palm Warblers appeared to feed particularly intensively in early morning and late afternoon. Blackpoll Warblers took longer rest pe-

riods, but foraged throughout the morning, and at an increased rate between 11:00 and 12:00—as did Tennessee Warblers. Blackpolls also fed after 15:00 until 17:00. Tennessee Warblers foraged very intensively in the morning, but we did not see them at all after noon either in the south or central areas. As we saw all other



TABLE 7. Use of arboreal plants by warblers during spring migration in a central Illinois area. (Listed in order of percentage of food taken from plant by warblers.)

Arboreal species	% Frequency of plant	% Larval biomass	All warblers observed		Tennessee Warbler	
			% Food	% Time	% Food	% Time
Black oak ( <i>Quercus velutina</i> )	0.55		42.77	24.33		
Elm (chiefly <i>Ulmus americana</i> )	12.16	6.20	15.96	8.09	1.62	50.86
Shingle oak ( <i>Q. imbricaria</i> )	12.17	32.27	14.59	39.04	41.42	50.46
Cherry (chiefly <i>Prunus serotina</i> )	8.74	8.13	12.59	9.07	0	2.41
Black walnut ( <i>Juglans nigra</i> )	9.07	1.78	7.89	13.53	56.96	36.27
Hawthorn ( <i>Crataegus</i> sp.)	7.74	4.43	5.64	3.38		
Red oak ( <i>Q. rubra</i> )	1.11	1.32	0.34	1.69		
Rose ( <i>Rosa</i> sp.)	4.87		0.22	0.50		
Honey locust ( <i>Gleditsia triacanthos</i> )	2.43		0	0.36		
Smooth sumac ( <i>Rhus glabra</i> )	8.96					
Sassafras ( <i>Sassafras albidum</i> )	8.07	0.34				
Hackberry ( <i>Celtis occidentalis</i> )	5.53	11.43				
Maples ( <i>Acer negundo</i> and <i>A. saccharinum</i> )	3.76	0				
Gray dogwood ( <i>Cornus racemosa</i> )	2.65	0.95				
Wild grape ( <i>Vitis</i> sp.)	1.22					
Other woody plants*	6.05	33.12				
Dead	5.09		0	0	0	0
Total number of plants = 865						

\* White ash, crab apple (*Malus* sp.), climbing bittersweet (*Celastrus scandens*), red cedar, cottonwood, pignut hickory (*Carya glabra*), shagbark hickory (*C. ovata*), honeysuckle (*Lonicera proliifera*), black locust (*Robinia pseudoacacia*), osage-orange (*Maclura pomifera*), poison ivy, redbud, bramble (*Rubus* sp.), green brier, nannyberry (*Viburnum lentago*), willow (*Salix* sp.), woodbine, and prickly-ash (*Zarhoxyllum americanum*).

common species both morning and afternoon, we believe that the Tennessees were not merely overlooked. The absence of afternoon foraging notwithstanding, Tennessee Warblers, for their size, ingested more food than did other warblers (Table 4). We have attributed the lows in their foraging rate at the forest edge to periods when warblers were at rest, and thus difficult to see.

## DISCUSSION

King (1974) reviewed the methods for studying energetic requirements of wild birds. We used a variation of time-activity study, a method based upon certain assumptions, whose validity remains to be proved. The major assumption is that the feeding and resting patterns observed were the same outside the observation period as within. Although we attempted

to observe foraging throughout the day, the actual time we had unobstructed viewing of warbler and prey was, on average, only 28 min per hour in the south, and 9 min per hour in the central area. The briefer viewing time in central Illinois was primarily due to low larval density, which in turn resulted in (1) more movement of birds as they foraged, and (2) more concealment by foliage. Both conditions increased the difficulty of observing foraging.

Populations of larvae were similar in forest-edge-shrub habitat, and adjacent forest interior (Fig. 2). There is no proof that birds foraged differently in the two habitats, and the flight between them would be very short for a warbler.

Our method has several other possible sources of error, but probably none as potentially important as the observations on size of

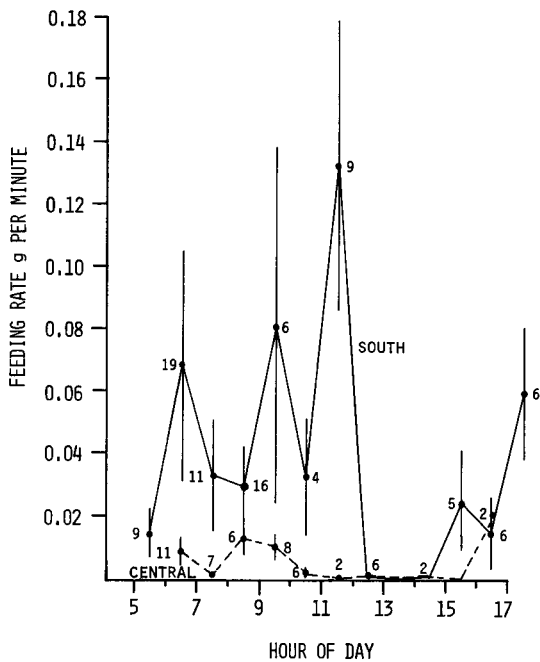


FIGURE 4. Daily pattern of feeding rates of all warblers observed in central (dashed line) and southern Illinois study areas in forest-edge and shrub habitat in May 1981. Numeral indicates the number of observations represented by a point. Vertical line indicates  $\pm 1$  SE for each sample.

prey. Different species of larvae have characteristic body forms—some being thin-bodied, and others fat—and shape has a marked effect on the weight-length relationship. The vast majority of larvae in our study areas (and those eaten by warblers) were neither very fat nor very thin species, although a few individuals of both types were present. When we plotted weight-length curves for the common species of leafrollers, geometrids, and fruitworms we found that larvae up to 15 mm fell close to the same line, but above 15 mm they diverged conspicuously (Fig. 1). To determine weight of small prey, size differentiation was more important than species differentiation. An observational error of 5 mm in larval size determination (i.e., 5 mm instead of an actual 10 mm) would be a very large percentage error for that observation especially when size was converted to weight, but it would amount to an error of only 10 calories in the final conversion. Many observational errors of 5 mm would show up as large errors in the final calorie value only if the errors were consistently lower or consistently higher than the actual larval length.

The birds we observed might have been particularly tame, and if tameness reflects metabolic rate then that could have caused bias. We were not aware of individual differences in tameness of warblers. In the south, where

food was abundant, warblers had little need to move around, and paid us little or no attention; in central Illinois, they moved almost constantly, not from fear of the observers, but to find food.

Most of our observations were brief (under 5 min). Analysis of the data revealed that average feeding rates were higher for short observations than for the longer observations (over 6 min). This was true because the short observations contained more periods of active feeding than of resting, and the longer periods almost always contained rest periods. We interpreted this to mean that we were missing birds at rest more often than birds actively feeding. During a long observation we saw the rest periods because we usually had the bird in view from the time it was actively feeding. Overall, our records indicated that birds were foraging 45–68% (e.g., Blackpoll: 54%) of the time during their active hours, but the data on individual birds showed that they were resting (in the south) generally longer than they were feeding (Table 4). Our figures for average feeding and resting period (Table 4) are based on our longest observations—periods of sufficient length to include a full bout of either activity. Inspection of the data indicated the shortest *complete* feeding and resting periods were, respectively, 4 and 7 minutes; therefore, the average feeding and resting periods were based on observations at least that long. Using data on average resting and feeding times, we calculated a correction factor for feeding rate by dividing the actual feeding period as percent of average feeding and resting periods by the observed feeding time as percent of total time. This factor was entered as a multiplier into the calculation of feeding rate per hour, and thus, of daily caloric intake (Table 4).

In the south, where larval biomass averaged 0.70 g per  $m^3$  on the dates of our foraging observations, warblers ingested 14.8–19.0 kcal per day (1.4–1.9 per g of warbler gross weight). In central Illinois, where larval biomass was 0.02 g per  $m^3$ , daily food intake was calculated to be 7.2 kcal per day (0.7 per g). Warblers in the south may have been near their capacity of food intake in an unlimited food supply, the intermittent rest periods being essential for digestion of the food consumed. Ingestion could presumably have proceeded through the extended midday rest period, however, thus increasing the daily intake as much as 25%. The weight of fresh food consumed by warblers in the south exceeded the gross weight of the bird (1.2–1.7  $\times$ ), but 80% of the food was water. Caterpillars may be easy to digest but the energetic cost of their digestion is unknown to us. Kale (1965) reported digestive efficiency of

marsh wrens on a mixed insect diet to range from about 73 to 78%.

Average ambient temperature on the days of our observation was 15.3°C in the south, and 11.5°C in the central area, so there was some energy cost for temperature maintenance, and more in the central area. The energetic requirement for (cage) existence for birds the size we observed in the south would be 11–13 kcal/bird/day, based on data presented by Pinowski and Kendeigh (1977). Free birds might expend more energy than this, and the cost of a migration flight would be additional. Nisbet (1963) estimated the caloric cost of flight in Blackpoll Warblers to be 1.02 kcal per hour. At that rate a 5-h overland flight (see temporal pattern of night migration in Lowery and Newman 1955) would cost 5 kcal, making the energy expenditure at least 16–18 kcal for a day (24 h) that included a migration flight. The energy cost of flight may be somewhat higher than the figure cited (see chapter 5 of Pinowski and Kendeigh 1977, also Nisbet 1963).

The problem of massive food ingestion (processing) faced by migrant warblers is distinct from that of a granivorous species. Olson and Kendeigh's (1980) study on the gross energy requirement of a 12.3-g sparrow (slightly larger than the warblers) indicated a value of about 12–13 kcal per bird-day at 15°C. The sparrow's food was only 13% water (Kendeigh 1949), and it achieved its gross energy intake with only about 3 g of food (26% of the bird's gross weight). The warblers had to process five times as much food for about the same calories, costing time, even with an unlimited food supply. The high water content of the larval food of migrant warblers may be beneficial as there is a significant water loss during migration (Hart and Berger 1972).

Counting the midday rest (Fig. 4), warblers in the south consumed little energy during much of the day. Since they obtained food easily, their energy balance would definitely have been positive, allowing for the accumulation of fat. In central Illinois, the warblers' food intake was below the energy requirements for the day; their behavior seemed consistent with a goal of energy conservation in a habitat with too little food. After vigorously searching for food in the early part of the morning, especially from tree-to-tree rather than branch-to-branch as in the south, warblers in the central area curtailed their search about 10:00. At the level of larval biomass available, it was advantageous for them not to expend energy in fruitless search. After 16:00 they foraged again, and apparently migrated that night, as we could find few migrants in the area on the following day (13 May).

Warblers in general, and Tennessee Warblers in particular, appeared to prefer leafrollers as food both in the south and central areas. Populations of leafrollers were about comparable in both areas (Table 2), thus the more positive metabolic balance of warblers in the south was dependent upon other groups of larvae—geometrids, fruit worms and others—all present at much higher densities in the south (Table 2). Leafrollers were small and so provided only a small part of the biomass. It was the geometrid irruption that provided migrants the required food.

Lepidoptera larvae constituted 95% of the total invertebrate biomass available on forest-edge foliage in the south, and 75% in the central. In either area the available biomass of invertebrates *other than* larvae (0.035 g/m<sup>3</sup> south, and 0.007 g/m<sup>3</sup> central, Table 2) would have been inadequate to support the migrants, based on the available caloric values of various invertebrates (Cummins 1967).

The phenomenon of pre-migratory fat deposition (Farner 1955, King 1972) implies that appropriate food resources are readily available, but the sources of lipid nourishment anywhere on the migration route have received little study. The importance of such fat reserves to migrants becomes obvious from our observations of warblers in central Illinois in spring 1981. Warblers and other migrants could "ride" the waves of spring caterpillar irruptions from the winter range northward if the irruptions were frequent enough to support the birds. In Illinois extensive irruptions of larvae occurred in the heavily forested southern tip of the state each spring, 1979–1981, but in the poorly forested central region only in 1979.

It may be essential for warblers to reach one or more irruptions of Lepidoptera in the course of their northward flights in order to have sufficient feeding efficiency to compensate for the large bulk of their food (80% water). Depending upon the pre-migration fat load, it may also be essential that warblers who reach areas with insufficient food resources keep their energy losses to a minimum and move as soon as possible to an area with more food. Rappole and Warner (1976) showed that those migrant warblers who maintained a positive weight balance remained in an area three days or longer, whereas most warblers (perhaps 90%) lost weight in the area and moved on. As these authors stated, it is adaptive for fat-depleted birds to continue their migration when they are unable to find, or compete for, food resources, their alternative being starvation. The importance of caterpillar irruptions to such migrants seems obvious. If such larval outbreaks are related to habitat availability, that

relationship must be understood if migrant populations are to be preserved in a time of rapid habitat loss.

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