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Temporal Patterns of Foraging Activity in Some Wood Warblers in Relation to the Availability of Insect Prey

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Summary. I monitored the temporal pattern of diurnal feeding activity in several wood warbler (Parulidae) species and concomitantly recorded the numbers of active (flying) insects in 2 willow habitats in the western United States. At one site the temporal relationship between the density of active and inactive (nonflying) insects was investigated. The diurnal patterns of insect and bird activity were inversely related and each pattern was significantly nonuniform throughout the day; the wood warblers were largely inactive during the middle of the day when insects were most active.

As foliage-gleaning birds, wood warblers depend primarily on the availability of inactive (nonflying) insects that they pick from the foliage, and they appear to be limited in their foraging activity by the unavailability of such insects during midday. Interestingly, the duration of midday inactivity for a given bird species varied inversely with the proportion of time that species spent flycatching. Thus, food availability may play an important role in determining the temporal patterns of feeding activity in these insectivorous bird species.

Introduction

Distinctive temporal patterns in the diurnal foraging activity of birds have been well described (for example: Morton 1967a; Mikkola 1970; Kessell 1976; Spurr 1978; Orians 1980) but the determinants of these patterns have been quite speculative. Among insectivorous bird species, a common pattern is one of a high level of feeding activity in the early morning, a decrease during midday, and another lesser increase in the late afternoon (Ricklefs and Hainsworth 1968; Ricklefs 1971; Diamond 1973; Dyer 1974; Austin 1978; Craig 1978; Greenwood and Harvey 1978; Ratkowsky 1978). The most frequent explanation for such a pattern is that the birds have problems dissipating the radiational heat load during midday and their feeding activity decreases concomitantly. This is almost certainly the case for those species whose food resource availability is unaffected by ambient temperatures, and the species are probably responding either to midday heat stress (Ricklefs and Hainsworth 1968; Spurr 1978) or, in some cases, to decreased metabolic demands during midday (Morton 1967a, b; Kessell 1976).

More recently, optimal foraging theory has led to the additional suggestion that the energetic costs and benefits of foraging should result in spatial and temporal adjustments in an individual's foraging behavior in response to nonuniform availabilities of prey in space and time (Pyke et al. 1977). The recent work of Holmes et al. (1978) and Orians (1980) points to the potential importance of such economic, as well as physiological constraints on the temporal patterns of foraging activity in birds. In this paper, I test the hypothesis that the temporal pattern of foraging activity in some wood warblers (Parulidae) is independent of food availability.

Materials and Methods

I monitored bird and insect activity in willow (*Salix* sp.) habitats in 3 localities within the USA: within the "south forty" area at the University of Montana Biological Station 10 km east of Polson, Montana (26 July 1978); within the "willow flats" area of Grand Teton National Park, Wyoming (22–30 May 1975); and along the Rio de Flag 10 km northwest of Flagstaff, Arizona (27–30 August 1976). Observations were recorded before (Wyoming) or after (Montana, Arizona) the nesting season, and individual birds were feeding only themselves.

Flying insects were sampled in all 3 sites by coating white 10 by 10 cm plastic boards with Tanglefoot™ and hanging them at the tips of willow branches at 0.5 m height intervals, to 2.5 m. Two 5-board stations were established at each site and the insects sampled at 1.5 h intervals from dawn to dusk on a single clear day. During each sampling period, I counted insects within the

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1–6 mm size range, picked them from the boards, and smoothed the Tanglefoot™ surface again.

Nonflying, or inactive, insects were sampled in the Arizona site on the same day that flying insect samples were taken by separately enclosing 4 willow branches every 2 h with 84 by 102 cm plastic bags, cutting the branches, and transporting the contents to the laboratory. I sprayed insecticide into each bag and later emptied the contents, counted the insects within 1–6 mm size range, and dried and weighed the vegetation.

I monitored bird activity at the Wyoming and Arizona sites by walking a 0.5 km by 40 m belt transect every 1.5 h (interspersed with the insect sampling in Wyoming, and on a separate day from insect sampling in Arizona) and recording the numbers of warblers of various species that were observed. Active birds are more likely to be censused and numbers observed should therefore reflect the level of their feeding activity (Orians 1980). The only small, foliage-gleaning species that were present in Wyoming at this time were the Yellow Warbler (*Dendroica petechia*), Yellow-rumped Warbler (*Dendroica coronata*), and Common Yellowthroat (*Geothlypis trichas*). In Arizona, Virginia's (*Vermivora virginiae*), Orange-crowned (*Vermivora celata*), Nashville (*Vermivora ruficapilla*), Yellow-rumped and MacGillivray's (*Oporornis tolmiei*) warblers were the only small, foliage-gleaning species present. Upon encountering a foraging warbler, the method of obtaining food (glean, sally, hover, probe) was also recorded in Wyoming. No more than 5 separate observations were recorded for a given individual before continuing on to the next bird.

In Montana, interspersed with insect sampling, I recorded the number of foraging sallies in 15 min as an estimate of feeding activity in the Willow Flycatcher (*Empidonax traillii*).

Results

Wyoming. Warbler foraging activity was significantly nonuniform throughout the day ($\chi^2 = 44.9$, $P < 0.001$). The diurnal pattern was one of a high activity level immediately after dawn, a decrease toward midday, and a slight increase once again in the early evening (Fig. 1). Flying insect activity also varied significantly with time of day ($F = 100.0$, $P < 0.001$). On the same day that warbler activity was monitored, insect activity was at its lowest level in the early morning before reaching a peak at 1,500–1,600 h and then decreasing to intermediate levels in the late evening (Fig. 1). Thus warbler activity and insect activity were inversely related ($r = -0.79$, $P < 0.01$).

With the activity curves of the 3 warbler species plotted separately, differences in the peaks of activity among species become apparent (Fig. 2). The Common Yellowthroat peaked first and was not observed again later in the day, the Yellow Warbler peaked next and showed a second peak in the evening, and the Yellow-rumped Warbler peaked latest in the morning and earliest in the afternoon.

The proportion of time each species spent sallying for aerial insects (flycatching) was recorded as 55% ($n = 122$) for Yellow-rumped Warbler, 26% ($n = 86$) for Yellow Warbler, and 0% ($n = 48$) for Common Yellowthroat.

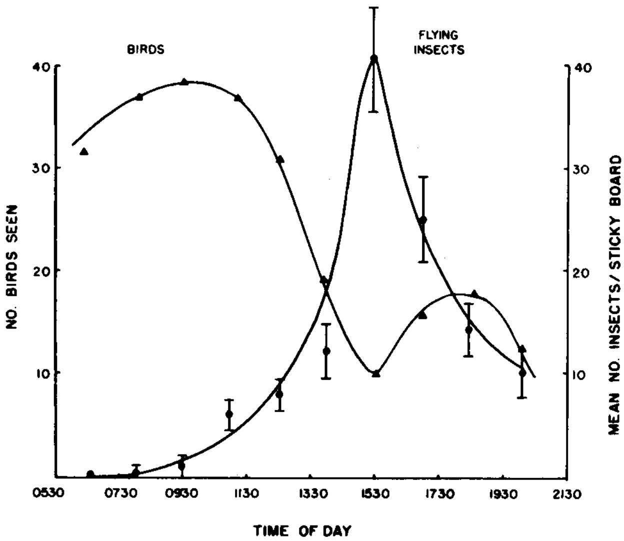

Fig. 1. The mean (±SE) number of 1–6 mm insects captured on 10 by 10 cm sticky boards (closed circles) and the number of warblers detected (closed triangles) during each of 10 daily time periods in the willow habitat of Wyoming

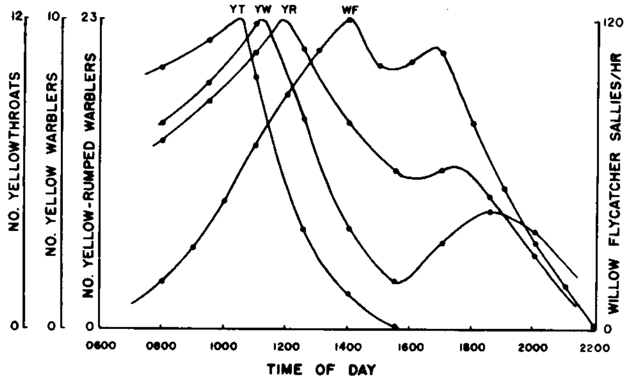

Fig. 2. The temporal pattern of feeding activity in Common Yellowthroats (*YT*), Yellow Warblers (*YW*), Yellow-rumped Warblers (*YR*), and Willow Flycatchers (*WF*). The heights of all curves have been adjusted so that the relative timing of peaks in activity can be more readily compared

Arizona. The general pattern of bird and insect activity was the same as described above although the peak in insect activity and decline in warbler activity occurred slightly earlier in the day (Fig. 3). Both bird ($\chi^2 = 30.4$, $P < 0.001$) and insect ($F = 87.2$, $P < 0.001$) activity varied significantly with time of day. The number of nonflying (inactive) insects sampled from the willow bushes also varied significantly with time of day ($\chi^2 = 36.3$, $P < 0.001$) and inversely with the numbers caught on the sticky boards (Fig. 3).

In order to determine the similarity in insect types sampled by the two methods, I identified the order to which individuals belonged for a sample of 12 willow branches collected early in the morning and for a sample of 3 sticky boards that were left out

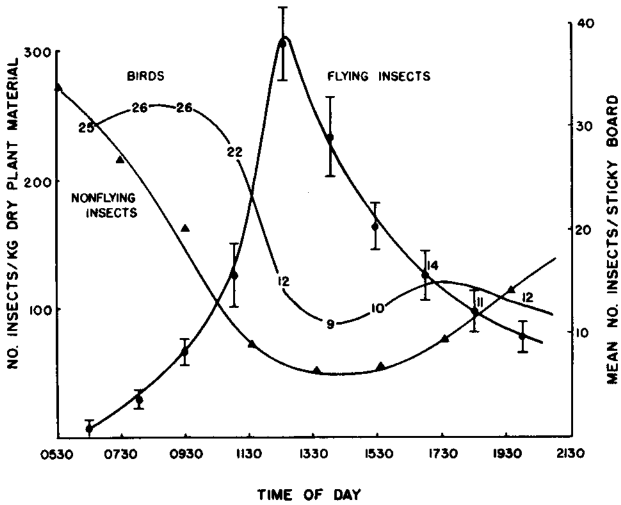

Fig. 3. The number of insects counted in combined plant samples (closed triangles), the mean ($\pm$SE) number of insects captured on 10 by 10 cm sticky boards (closed circles), and the numbers of warblers detected (broken line) during various time periods throughout the day in the willow habitat of Arizona. Numerals in the warbler activity curve indicate the numbers of individuals detected

Table 1. The number of individual insects belonging to each of several orders for willow and sticky board samples from Arizona

Order	Willow branches	Sticky boards
Diptera	55	86
Hemiptera	7	26
Neuoptera	4	13
Coleoptera	6	9
Hymenoptera	2	8
Homoptera	4	–
Lepidoptera (larvae)	4	–

for 24 h. In each case, dipteran and hemipteran insects made up greater than 75% of the sample (Table 1).

Montana. The pattern of diurnal insect activity was also nonuniform ($F=98.3$, $P<0.001$) and resembled closely the pattern and time of peak activity in Wyoming ($r=0.96$). Willow Flycatcher feeding activity (as measured by the number of sallies/h) increased to a bimodal peak in the afternoon and then declined through the evening (Fig. 2).

Discussion

The diurnal pattern of insect activity corresponds well with the temporal patterns that have been described for other north temperate areas (Adams 1941; Holmes et al. 1978). The diurnal pattern of warbler foraging activity also matches that described previously for other insectivorous bird species (cited earlier). Warbler activity is not independent of the abundance of insects as assessed by sticky boards, and upon initial inspection it appears that there is little agreement between warbler activity and insect abundance. However, sticky boards capture active (flying) insects while warblers (for the most part) do not. Insect abundance as measured by sticky boards should, therefore, be inversely related to the availability of insects to these foliage-gleaning birds. This expectation is borne out by the insect samples taken directly from the willows (Fig. 3). Insects are most abundant on the bushes when least abundant in the air, and warbler activity actually corresponds quite well with insect availability. Whether the insects caught on sticky boards were actually the same ones that served as available prey to the warblers is unknown, but a comparison of the insect orders present in the Arizona willow samples with the insect orders caught on sticky boards showed that, in each case, greater than 75% of the sample was composed of dipteran and hemipteran insects.

The birds seem to be constrained at the extremes of their activity curve by an inability to see under low light conditions (Kacelnik 1979), and constrained in the middle of the day by the relative unavailability of insects. Consistent with the idea that low light levels set the limits on foraging activity early and late in the day is the fact that a brief period of vigorous song occurs in most passerine bird species just before dawn (Welty 1975). This dawn chorus may represent a release from the competing demand of feeding since light levels are still too low for foraging purposes.

Empirical support for the view that the midday lull in feeding activity is a result of decreased food availability comes from an analysis of the activity patterns of the 3 warbler species that made up the composite activity curve of Fig. 1. When plotted separately, the curves of these 3 species reveal peaks of activity that differ among species, and that correspond well with the proportion of time they spend sallying for aerial insect prey (Fig. 2). It appears as if those species that have it in their behavioral repertoire to sally a lot are able to forage for a relatively extended period in the morning and to begin late afternoon activity a bit sooner than those species that glean insects from vegetation almost exclusively. In other words, the feeding activities of Yellow-rumped and Yellow warblers, both of which spend a good bit of time flycatching, seem less constrained by the insect activity during midday than that of the Common Yellowthroat, which was never observed flycatching.

By these same arguments, one might expect a flycatcher to have an activity pattern that corresponds even more closely with insect aerial activity. Since the patterns of insect activity in Montana and Wyoming were very similar, I superimposed activity curves of the Willow Flycatcher and the 3 warbler species (Fig. 2) to show that the flycatcher peaks later than the warblers and its afternoon resurgence occurs earlier as well. Dyer (1974) described a similar temporal pattern for Eastern Kingbirds. The persistence of a decrease in flycatcher activity during midday is apparently unrelated to food availability and may reflect thermoregulatory problems, or may reflect the fact that feeding rate exceeds digestive rates at this time and the birds become "full" (Holling 1966). Still other insectivorous bird species (nesting blackbird species) show a continuous increase in feeding activity toward midday and a subsequent decline without another resurgence (Orians 1980). Orians believes that food availability is an important determinant of the blackbird activity pattern and perhaps the reason he failed to observe a midday lull in feeding activity was because the birds' feeding rates never exceeded the digestive rates of those utilizing the food (in this case, parents plus young).

Since all bird species do not show bimodal feeding activity curves, it becomes unlikely that the commonly observed peaks in feeding activity early and late in the day merely represent, respectively, a response to, and an anticipation of, nightly food deprivation.

In conclusion, the temporal patterns of insectivorous bird activity and insect abundance are not independent and it is likely that food availability plays an important role in determing the temporal patterns of feeding activity in these insectivorous bird species (see Davies (1976) and Mikkola (1970) for similar conclusions).

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