

PARENTAL FEEDING OF NESTLING YELLOW WARBLERS IN RELATION TO BROOD SIZE AND PREY AVAILABILITY

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ABSTRACT.—The feeding by adult Yellow Warblers (*Dendroica petechia*) of nestlings in broods of 3, 4, or 5 young was studied during two breeding seasons on the forested dune ridge near Delta, Manitoba. Broods of 2-day-old young were selectively fed geometrid larvae by the adults, and broods of 8-day-old young were selectively fed chironomids and geometrid and other Lepidoptera larvae. The diet varied among broods of 3, 4, and 5 young at both ages, but this variation did not appear to affect the growth rates of the young. The total weight of items brought per half hour increased with brood size among broods of 2-day-old young. Broods of four 8-day-old young were fed the greatest amount of food. The diet of the nestlings is contrasted with the diet of adult Yellow Warblers observed in the same locality. Received 15 October 1980, accepted 19 October 1981.

THE Yellow Warbler (*Dendroica petechia*), along with six other species of primarily insectivorous passerines, nests densely on the forested dune ridge that separates Lake Manitoba from the Delta Marsh, Manitoba. Both the adults and nestlings of the species studied so far in this area are apparently sustained by a superabundant food resource, adult midges (Diptera: Chironomidae) (Busby and Sealy 1979, Biermann 1980, Sealy 1980). The greatest demand on the food resources in the ridge community probably occurs during the period when the young are being reared. It is important, therefore, to determine the diets of nestlings of the species in this community in relation to the food resources that are available at this time. We did this for the Yellow Warbler, and we examined the rates at which adults fed their young in broods of 3, 4, and 5 at two ages. To determine the effects of any feeding differences that might have been observed, we also measured the growth rate of the young. The diet of the nestlings relative to the prey available was also contrasted to that of adult Yellow Warblers studied on the same area by Busby and Sealy (1979). As the diet of nestlings of most parulid species is poorly known, beyond the general knowledge that they are insectivorous, our study fills in a gap for the Yellow Warbler in one area.

METHODS

We studied parental care in a densely nesting population of Yellow Warblers during the summers of

1978 and 1979 on a portion of the forested dune ridge that separates Lake Manitoba from the Delta Marsh, about 5 km west of Delta (50°11'N, 98°19'W), Manitoba. Willows (*Salix amygdaloides* and *S. interior*), Manitoba maple (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*) account for over 95% of the tree flora and provide a forest canopy about 10–14 m in height (see MacKenzie 1979). The prominent shrubs are elderberry (*Sambucus pubens*), dogwood (*Cornus stolonifera*), and raspberry (*Rubus ideaus*) (see Goosen 1978, Busby and Sealy 1979).

We located 139 active Yellow Warbler nests and recorded their contents each day during egg-laying and every 3–4 days thereafter. Observations were made at 19 nests with broods of 3, 4, or 5 young on day 2 (young young, YY) and day 8 (old young, OY) after the first chick in each brood had hatched. At 10 nests at least one parent was color-banded, at 5 nests neither parent was banded, and at the other 4 nests at least one parent was aluminum banded. Adults at each nest were separable by plumage differences.

Four nests of each of the three brood sizes at each age were observed (except that 3 nests with broods of five 8-day-old young and 7 nests with broods of three 2-day-old young were observed). Most of the nests observed were less than 2 m above the ground. Observations were made from a blind placed 1–2 m from the nest the day before observations were begun, at four times of the day: 0630–0830, 1000–1200, 1530–1730, and 1830–2030 (CDT). Observations spanned 12 June to 1 July in 1978 and 20 June to 19 July in 1979. Parental activities at or near the nest and the number and identity of prey items fed to the young were recorded. Large insects that protruded from the parents' bills could be identified, but small items could not. Therefore, the prey we identified were biased toward larger sizes. Items brought were unidentifiable in 347 of 1,211 feeding trips observed,

TABLE 1. Feeding rates and food loads (mean \pm SE) of Yellow Warbler parents.

| Age and number of young | Trips/half hour | | Items/trips | |
|------------------------------------|----------------------------|---------------|----------------------------|---------------|
| | Males | Females | Males | Females |
| 3YY ^a (48) ^b | 1.9 \pm 0.2 ^c | 1.0 \pm 0.2 | 1.2 \pm 0.1 | 1.2 \pm 0.1 |
| 4YY (32) | 2.6 \pm 0.2 ^c | 1.6 \pm 0.2 | 1.3 \pm 0.1 | 1.2 \pm 0.1 |
| 5YY (36) | 3.1 \pm 0.3 ^d | 0.9 \pm 0.3 | 1.2 \pm 0.1 ^d | 1.0 \pm 0 |
| 3OY (32) | 3.8 \pm 0.5 | 3.4 \pm 0.2 | 1.9 \pm 0.1 | 1.5 \pm 0.1 |
| 4OY (31) | 5.2 \pm 0.5 ^c | 2.7 \pm 0.4 | 2.6 \pm 0.1 | 2.2 \pm 0.2 |
| 5OY (32) | 4.2 \pm 0.3 ^d | 5.6 \pm 0.5 | 1.5 \pm 0.1 ^c | 1.2 \pm 0.1 |

^a YY (young young) refers to 2-day-old young; OY (old young) refers to 8-day-old young.

^b Number of half-hour observation periods in parentheses.

^c $P < 0.01$ between males and females.

^d $P < 0.025$ between males and females.

due in part to their smaller size, but also because the parents' positions while feeding the young obscured our view.

In 1979, 27 8-day-old nestlings were collected, and 70% ethanol was injected immediately into their esophagi. The stomach contents were removed within an hour and stored in ethanol. Food items were identified later in the laboratory using a variable-power microscope. Intact prey items were few in the samples, but head capsules, thoraxes, wings, occipital rings, and mandibles could be identified to order and often to family. This method probably biases results toward insects with thick hard coverings. The prey items observed being fed were compared to the prey items in stomachs to assess potential bias.

The foliage arthropod fauna of a 100-m line transect of a portion of the study area was sampled using a standard insect sweep net, in the manner described by Busby and Sealy (1979). They found that this method yielded representative samples when assessing the availability of arthropods to adult Yellow Warblers on this study area. The fauna was sampled in the morning and evening of every fifth day during the observation periods. The samples were sorted and identified to order or family and grouped into five categories to permit comparison with the prey being fed to the nestling warblers. These groups were: Chironomidae and Culicidae (midges and mosquitoes), Geometridae larvae (inchworms), all other Lepidoptera larvae, all other Diptera, and all other insects and arthropods.

The dry weights (to the nearest 0.1 mg) of the separate samples of midges, mosquitoes, and larvae were determined after being oven-dried at 60°C for one week. The two groups of larvae were then combined, and the protein content of the larvae and the chironomid and culicid samples was determined by the Manitoba Department of Agriculture.

Yellow Warbler nestlings in randomly chosen nests were weighed to the nearest 0.1 g between 2030 and 2130 (CDT) on a triple-beam balance. Nestlings could be weighed until day 6 post-hatching, after

which they jumped out of the nest following handling.

Statistical tests used include analysis of variance (ANOVA), linear regression, Chi-square, and Wilcoxon sign rank test. The level of significance used was $P \leq 0.05$.

RESULTS

Feeding rates and food loads.—Time of day had no effect on the feeding rate of adult Yellow Warblers with young of either age. Broods of five 2-day-old young were fed significantly more often by males than were smaller broods (Table 1). Males with 8-day-old young fed broods of 4 young more often than broods of 5 or 3. Among females, the only significant result was that broods of five 8-day-old young were fed more often than were smaller broods [(two-way ANOVA: males with YY-brood size, $F(2, 104) = 6.16$; time of day, $F(3, 104) = 2.47$; males with OY-brood size, $F(2, 83) = 2.94$; time of day, $F(3, 83) = 0.71$; females with YY-brood size, $F(2, 104) = 2.52$; time of day, $F(3, 104) = 1.40$; females with OY-brood size, $F(2, 83) = 11.04$; time of day, $F(3, 83) = 2.30$].

The number of items brought per trip by males and females with 2-day-old young was constant throughout the day and did not vary among the different brood sizes [Table 1; two-way ANOVA: males—brood size, $F(2, 229) = 0.77$; time of day, $F(3, 229) = 0.76$; females—brood size, $F(2, 76) = 1.43$; time of day, $F(3, 76) = 1.50$]. Males feeding 8-day-old young brought the largest loads to broods of 4 (Table 1) and generally brought larger loads in the early morning and smaller loads in the late afternoon [two-way ANOVA: brood size, $F(2, 273) = 30.04$; time of day, $F(3, 273) = 3.51$].

TABLE 2. Number of insects in each group observed being fed by adult Yellow Warblers to young in three brood sizes at two ages.

| Insect group | Brood size and age | | | | | | | | | | | |
|--------------------------------------|-------------------------|------------|------------|------------|------------|-------------|-------------|-------------|------------|-------------|-------------|-------------|
| | 3 YY | | 4 YY | | 5 YY | | 3 OY | | 4 OY | | 5 OY | |
| | ♀♀ (48) ^a | ♂♂ (91) | ♀♀ (52) | ♂♂ (83) | ♀♀ (32) | ♂♂ (111) | ♀♀ (108) | ♂♂ (121) | ♀♀ (82) | ♂♂ (159) | ♀♀ (178) | ♂♂ (134) |
| Chironomids and culicids (I) | 22 | 28 | 26 | 29 | 1 | 34 | 68 | 110 | 117 | 247 | 95 | 73 |
| Geometrid larvae (II) | 8 | 48 | 15 | 42 | 18 | 91 | 10 | 37 | 6 | 17 | 34 | 49 |
| Other larvae (III) | 1 | 2 | 0 | 0 | 0 | 2 | 2 | 8 | 1 | 2 | 1 | 3 |
| Other Diptera (IV) | 1 | 0 | 1 | 1 | 3 | 5 | 5 | 1 | 5 | 1 | 0 | 1 |
| All other insects (V) | 1 | 0 | 1 | 1 | 0 | 5 | 5 | 6 | 13 | 51 | 15 | 5 |
| Feeding trips with unidentified prey | 19 | 16 | 15 | 21 | 10 | 7 | 42 | 43 | 21 | 42 | 55 | 44 |

^a Total number of feeding trips observed.

Females fed broods of four 8-day-old young the largest number of items per trip (Table 1) and did not vary their rate with time of day [two-way ANOVA: brood size, $F(2, 238) = 25.91$; time of day, $F(2, 238) = 1.74$].

Males fed 2-day-old young more often than females regardless of brood size [ANOVA: broods of 3, $F(1, 94) = 8.54$; broods of 4, $F(1, 62) = 7.97$; broods of 5, $F(1, 70) = 29.95$]. With 8-day-old young, males and females fed broods of 4 at equivalent rates [$F(1, 62) = 0.68$], males fed broods of 3 more often than their mates did [$F(1, 60) = 14.3$], and females fed broods of 5 more often than males did [$F(1, 62) = 5.33$]. Both sexes fed 8-day-old young more often than 2-day-old young [females—broods of 3, $F(1, 78) = 61.9$; broods of 4, $F(1, 61) = 5.04$; broods of 5, $F(1, 66) = 69.0$; males—broods of 3: $F(1, 78) = 15.6$; broods of 4, $F(1, 61) = 22.3$; broods of 5, $F(1, 66) = 6.9$].

Males with 5 young brought a larger food load per trip than did females at both ages of nestlings studied. No other significant differences between parents were observed [ANOVA: 3YY, $F(1, 102) = 0.63$; 4YY, $F(1, 97) = 1.02$; 5YY, $F(1, 124) = 5.39$; 3OY, $F(1, 142) = 0.68$; 4OY, $F(1, 176) = 3.40$; 5OY, $F(1, 211) = 10.3$].

All parents except females with 5 young brought greater load sizes when feeding older young [females—broods of 3, $F(1, 93) = 8.27$; broods of 4, $F(1, 96) = 17.09$; broods of 5, $F(1, 143) = 3.52$; males—broods of 3, $F(1, 151) = 53.1$; broods of 4, $F(1, 177) = 52.5$; broods of 5, $F(1, 192) = 7.94$].

When the young were 2 days old, more food items were brought by males than by females. Overall, 2-day-old broods of 4 were fed more food items than broods of 5 or 3. When the young were 8 days old, more food items were brought by males to broods of 3 and 4 than by females, while the reverse was true for broods of 5. Overall, broods of 4 were fed more items than broods of 3 or 5 at this age.

Food items available and used.—As time of day did not affect the type of prey the adults brought to the young (Chi-square, $P > 0.05$ in 10 of the 12 cases), the observations from all time periods were combined. At each age, significant differences in the proportion of each of the five insect groups in the diet brought by females were observed among brood sizes (Table 2; YY: $\chi^2 = 30.6$, 8 df; OY: $\chi^2 = 36.3$). At both ages, females with 5 young brought more geometrid larvae and fewer chironomids and culicids than did females with broods of 3 and 4 young. There were also significant differences between 2- and 8-day-old young in the proportion of items brought by females with broods of 4 and 5 young (broods of 3: $\chi^2 = 4.2$, 4 df; broods of 4: $\chi^2 = 29.9$, broods of 5: $\chi^2 = 38.1$). A larger proportion of chironomids and culicids and a smaller proportion of geometrid larvae were fed to the older young in broods of 4 and 5, but females that were feeding broods of 3 maintained a relatively constant diet between the two ages.

The proportion of insects in each group observed being fed by males (Table 2) differed significantly among brood sizes at each age

TABLE 3. Total number of insects in each group found in the stomachs of nine 8-day-old warbler nestlings in each brood size.

| Insect groups ^a | Brood size | | |
|----------------------------|------------|-----|----|
| | 3 | 4 | 5 |
| I | 76 | 109 | 71 |
| II | 28 | 17 | 21 |
| III | 2 | 4 | 4 |
| IV | 14 | 5 | 10 |
| V | 13 | 15 | 16 |

^a See Table 2.

(YY: $\chi^2 = 20.5$, 8 df; OY: $\chi^2 = 103.4$). Again, broods of 3 and 4 were fed more chironomids and culicids and fewer larvae than broods of 5. The proportion of items in each group brought by males also differed significantly between the two ages (broods of 3: $\chi^2 = 34.3$, 4 df; broods of 4: $\chi^2 = 130.5$; broods of 5: $\chi^2 = 30.3$) and followed a trend similar to that of the females.

Intersexual differences in the proportion of items observed being fed to the nestlings were also significant, except between parents feeding four 2-day-old young (3YY: $\chi^2 = 12.7$; 4YY: $\chi^2 = 5.5$; 5YY: $\chi^2 = 10.3$; 3OY: $\chi^2 = 13.7$; 4OY: $\chi^2 = 10.8$; 5OY: $\chi^2 = 11.2$; all have 4 df). Males generally brought more geometrid larvae than did females. Females brought more chironomids and culicids.

The proportions of items observed being fed to nestlings and those in the stomachs (Table 3) differed significantly in each brood size, mainly due to differences in the proportion of insects in groups IV and V. These insects were usually small and were underestimated in the field. The stomach contents of the young in the three brood sizes were not significantly different ($\chi^2 = 13.5$, 8 df), although the trend found is similar to the field-observed diet in that the largest proportion of chironomids and the smallest proportion of larvae were fed to broods of four.

The prey items fed are compared in Figs. 1 and 2 to prey items available in each sampling period. Although the total number of insects varies, the relative importance of each group remained fairly constant throughout the observation periods. A Wilcoxon sign test was used to compare the proportion available in each group to the proportion (by number) of that group observed to have been fed. Adult

Yellow Warblers selected geometrid larvae ($P = 0.016$) and avoided feeding all other larvae ($P = 0.031$) and all other insects ($P = 0.016$) when feeding 2-day-old young. Adults feeding 8-day-old young selected chironomids and culicids ($P = 0.008$), geometrid larvae ($P = 0.008$), and other larvae ($P = 0.063$) and avoided all other Diptera ($P = 0.016$) and all other insects ($P = 0.008$). Thus, adult Yellow Warblers selected particular prey items as food for their nestlings.

Weight and protein content of nestling food.—The average dry weights of insects in groups I, II, and III were 3.1, 6.0, and 8.5 mg, respectively (Biermann 1980). The weight of an "average" insect fed to a nestling was calculated for each parent with each brood size at each age by multiplying the number of individual prey items of each group being fed (Table 2) by the average weight of insects in that group, summing for groups I, II, and III and dividing by the total number of insects in the three groups. This estimate, multiplied by the total number of insects brought per half hour (Table 1) yields an estimate of the average weight of food items brought per half hour (see Table 4). Because the items observed being fed were biased toward larger prey, the true weight of food brought per half hour was smaller. As the number of feeding trips in which prey were unidentified was relatively constant (usually about one-quarter to one-third of the feeding trips, Table 2), however, the values calculated are useful in comparing the feeding rates.

Generally, males brought heavier prey items than did females. Heavier items were brought to 2-day-old young than to 8-day-old young, because a larger proportion of the diet of 2-day-old young was Lepidoptera larvae. Males feeding 2-day-old young brought more food to larger broods. Females fed 2-day-old young at a rate unrelated to brood size. Females brought more food to larger broods of 8-day-old young than to smaller broods. Males did not. Overall, at 8 days, broods of 4 were fed more food by weight than were broods of 5 or 3.

Other factors apparently are also important. The fat, ash, protein, and water content of insects, as well as their digestibility, may affect the proportion of the dry weight that is usable by the nestling. The proportion of dry weight that is protein was 59.8% and 62.6% for the chironomids and larvae, respectively. Protein content is likely to be the most important com-

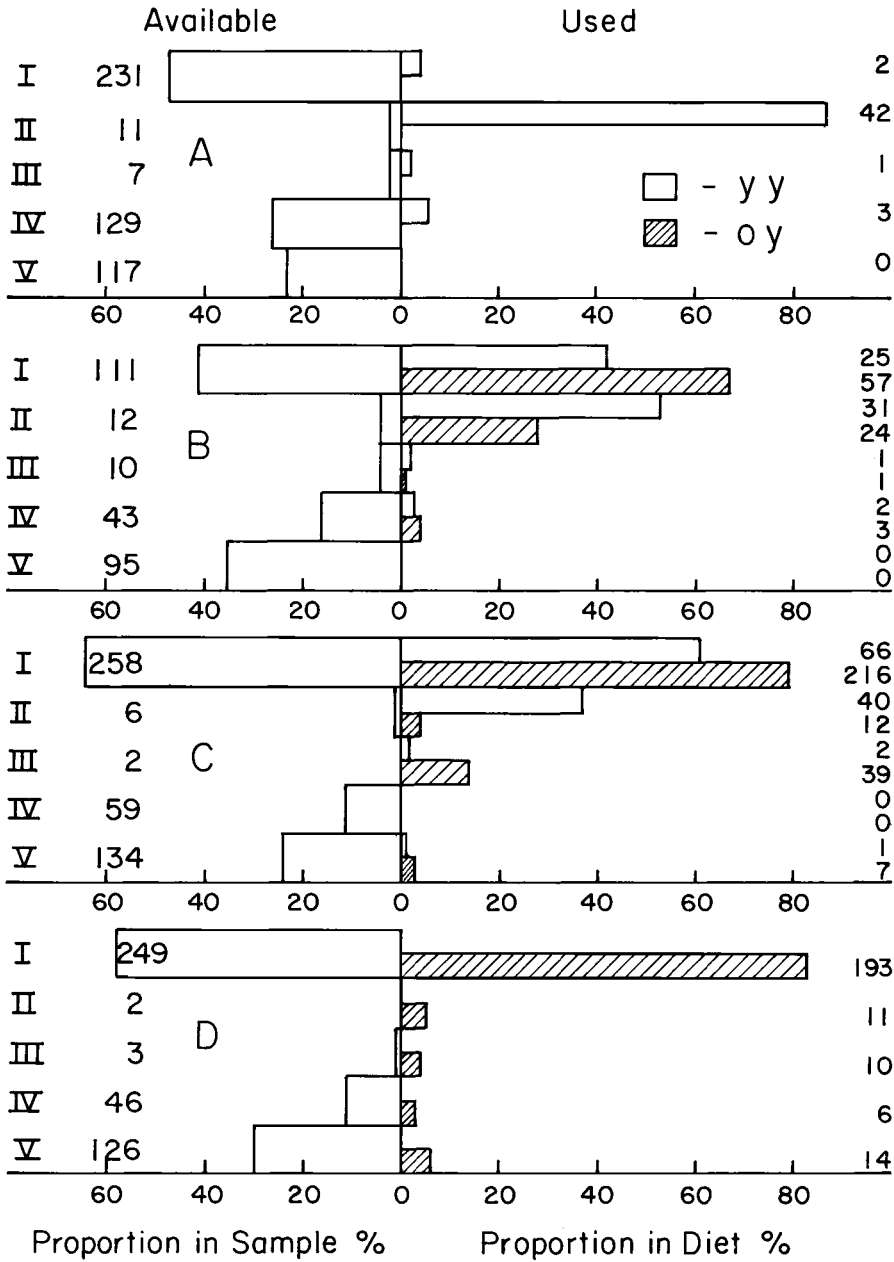


Fig. 1. Proportion, by number, of insects in groups I-V in sweep net samples, and the proportion of insects in each group observed being fed to 2- and 8-day-old Yellow Warblers in 1978. A, 12-16 June; B, 17-22 June; C, 23-27 June; D, 28 June-1 July. Absolute numbers of insects are given on the sides.

ponent of a nestling's diet, because rapid body growth occurs during this stage of development (Kear 1972).

The average dry weight of the insects was multiplied by the proportion of the weight that

is protein to determine the amount of protein in the insects. The total weight of protein fed by the parents of the nestlings at each age and in each brood size was determined using calculations described above (Table 4). Compar-

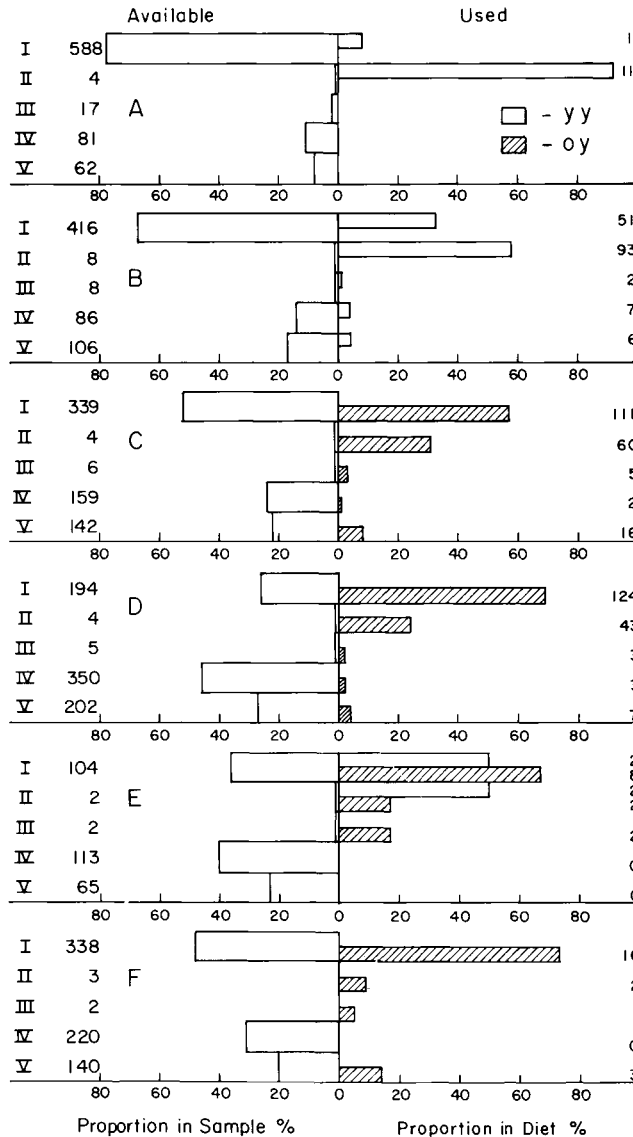


Fig. 2. Proportion, by number, of insects in groups I-V in sweep net samples, and the proportion of insects in each group observed being fed to 2- and 8-day-old Yellow Warblers in 1979. A, 20-24 June; B, 25-29 June; C, 30 June-4 July; D, 5-9 July; E, 10-14 July; F, 15-19 July. Absolute numbers of insects are given on the sides.

isons among brood sizes are similar to those described for the dry weight of food brought by the parents, but the differences in the amount fed among the brood sizes are generally decreased.

Growth rates.—As broods of 3, 4, and 5 young are fed different proportions of food items at different rates on a per nestling basis, these differences might be expected to affect

the growth rates of the young. Fig. 3 shows the growth rate, measured as change in body weight, of nestlings in broods of 3, 4, and 5. Because the same nestlings were not weighed every day and the weights shown are means of all nestlings weighed, the curves do not conform exactly in shape to standard growth curves. The overall growth rates of young in the brood sizes can be compared using the

TABLE 4. Average dry weight (mg) and protein content (mg) of insects fed by male and female parent Yellow Warblers to broods of 3, 4, and 5 young at two ages.

| Brood size and age | Average dry weight of average insect brought | | Average dry weight of food brought per half-hour | | Mean dry weight of protein per average item | | Average dry weight of protein brought per half-hour | |
|--------------------|--|---------|--|---------|---|---------|---|---------|
| | Males | Females | Males | Females | Males | Females | Males | Females |
| 3 YY | 5.0 | 4.0 | 11.6 | 4.8 | 3.2 | 2.5 | 7.4 | 3.0 |
| 4 YY | 4.8 | 4.2 | 16.4 | 7.9 | 3.0 | 2.2 | 10.2 | 4.2 |
| 5 YY | 5.3 | 5.9 | 19.5 | 5.3 | 3.3 | 3.7 | 12.2 | 3.3 |
| 3 OY | 4.3 | 3.6 | 30.8 | 18.4 | 2.5 | 2.2 | 18.0 | 11.2 |
| 4 OY | 3.3 | 3.3 | 45.8 | 19.4 | 2.0 | 2.0 | 27.0 | 11.8 |
| 5 OY | 4.4 | 3.9 | 27.5 | 26.1 | 2.7 | 2.4 | 17.0 | 16.1 |

regression equations provided in Fig. 3. A test for the equality of slopes (Sokal and Rohlf 1969) showed no significant difference in the growth rate of the young in the three brood sizes [AN-OVA: $F(2, 11) = 0.65$]. Using a graphical technique to convert the growth curve to a straight line (Ricklefs 1967), we calculated the specific growth rate constant (K) for young in each brood size, using a weight asymptote of 11.0 g. The rate constants (0.546, 0.551, and 0.541 for broods of 3, 4, and 5 young, respectively) again suggested similar growth rates of young in the three brood sizes.

DISCUSSION

FEEDING RATES AND FOOD LOADS

Time of day.—Time of day did not usually affect the feeding rate and load size of adult Yellow Warblers feeding their young. In many species, most feeding usually occurs just after dawn and at dusk, and the least occurs at mid-day or mid-afternoon (Best 1977, Nolan 1978, Pinkowski 1978). These variations are usually related to differences in the activities of the prey species, as many insects are most active in the coolest parts of the day, or are associated with the need of the birds to feed heavily just before and after the overnight fast. The diet of some bird species may also vary with time of day (Walsh 1978). In the present study, however, early-morning sampling was not done just after dawn, nor was evening sampling done just before sunset. The lack of dietary variation during the day indicates that insect activities did not greatly affect the foraging success of the birds.

Brood size and age.—Generally, adult feeding rate increases with an increase in brood size

(Moreau 1947, Lack and Silva 1949, Lack and Lack 1951, Royama 1966, Morehouse and Brewer 1968, Hussell 1972, Best 1977, Walsh 1978). The feeding rate of adult Yellow Warblers was greatest in the largest brood size when broods were 8 days old. Food loads, however, were not the largest (Table 1). At 2 days of age, both feeding rate and food-load size were greatest for broods of 4.

Other workers have also found that feeding rate is not directly related to brood size. Pinkowski (1978) found no positive relation between brood size and feeding rate by either male or female Eastern Bluebirds (*Sialia sialis*). Seel (1969) found that the feeding rates for broods of 3, 4, and 5 House Sparrows (*Passer domesticus*) did not differ significantly.

Feeding rates were shown in our study and by several others to increase as the nestlings grew older (Gibb and Betts 1963, Royama 1966, Seel 1969, Nolan 1978, Pinkowski 1978, Walsh 1978). Larger young generally require more food to supply sufficient energy for thermoregulation and developmental processes.

The role of males relative to females in feeding the young varies among species. Nolan (1978) found that female Prairie Warblers (*D. discolor*) assumed a slightly larger proportion of the feeding duties, whereas Field Sparrows (*Spizella pusilla*) share this duty nearly equally (Best 1977). On our study area, male Yellow Warblers usually assumed the larger proportion of feeding duties.

Gibb and Betts (1963), Royama (1966), and Morehouse and Brewer (1968) noted that the feeding rate and the size of items brought were inversely related. Nolan (1978) found that adult Prairie Warblers brought similar sized food items, but, as the young grew older, both the

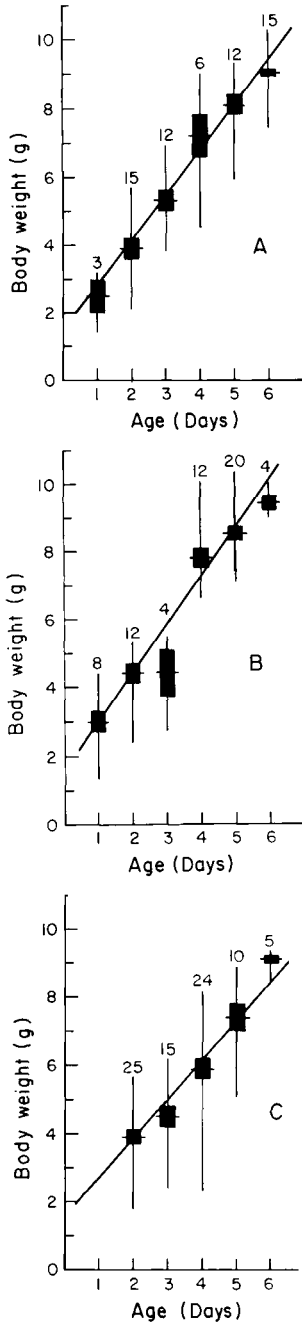


Fig. 3. Growth curves of Yellow Warblers in broods of 3 (A), 4 (B) and 5 (C) young. The horizontal lines are the mean weights, the vertical lines the ranges, and the solid bars denote 1 SE on each side of the mean. The numbers above each vertical line are sample sizes. Regression equations: 3 young, $y = 1.38 + 1.31x$; 4 young, $y = 1.56 + 1.39x$; 5 young, $y = 1.30 + 1.20x$. The slopes of all regression equations are significantly different from zero.

feeding rate and the size of items fed increased. Thus, he observed no inverse correlation between feeding rate and the size of items fed. In the Yellow Warbler, males brought heavier items and fed the young more often. Within each sex, however, the inverse relation between feeding rate and food size held.

DIET OF NESTLINGS

Busby and Sealy (1979) found the diet of adult Yellow Warblers during the breeding season at Delta to be composed mainly of Diptera, particularly chironomids. Studies of the diet of adult Yellow Warblers in other areas have found Hymenoptera or Homoptera and Coleoptera to be the major components of the diet (Kendeigh 1947, Frydendall 1967). Adult Yellow Warblers apparently are flexible in their choice of food and forage opportunistically (Busby and Sealy 1979).

Adult chironomids and culicids and larval geometrids were the main components of the diet of nestling Yellow Warblers. The proportion of these items in the diet changed with the nestlings' age. Two-day-old young were fed more geometrid larvae than were 8-day-old young, with a corresponding change in the proportion of chironomids and culicids. Stomach analyses confirmed, to an extent, feeding observations and indicated that chironomids, not culicids, were the most important insect in group I. Apparently, the abundant chironomids are an important source of nourishment for both adult and nestling Yellow Warblers during the breeding season at Delta.

Diet and prey availability.—Generally, adult Yellow Warblers did not feed their nestlings prey in proportion to its availability. They were selective. At both nestling ages, geometrid larvae were fed in proportions greater than were available. Other studies of passerine nestling feeding have found Lepidoptera larvae to be important components of the diet (Best 1977, Pinkowski 1978). In the present study, all other larvae and all other insects were under-represented in the diet of 2-day-old young, compared with what was available. When 2-day-old young were fed a geometrid larva, the parents often passed it back and forth between themselves and pulled on it, breaking it into smaller, more manageable pieces that were then fed to the nestlings. Attempts to feed

a larva whole to the nestlings usually failed. Because other larvae are usually wider and heavier than geometrid larvae, they would have required even more processing by the parents before they could be fed to the young. Probably more effort is required than is practical. Best (1977) found that girth rather than length limited the size of food that young Field Sparrows could ingest. Several studies have shown that the size of food items increases with nestling age, suggesting that the relative size of the nestlings and the food may be important (Gibb and Betts 1963, Best 1977, Nolan 1978, Pinkowski 1978, Walsh 1978, Johnson et al. 1980). All other insects collected in the insect samples included many hard bodied insects such as Coleoptera, Hymenoptera, and Hemiptera, all of which may have been unsuitable food for young birds.

Chironomids and culicids and all other larvae were selected preferentially for 8-day-old young, as were geometrid larvae. At 8 days of age, the nestlings are nearly adult size and can swallow larger larvae whole. Chironomids and culicids have soft abdomens that are easily digested, and, because they move slowly, several can be brought to the nest in one trip. Part of the body, however, is enclosed in a chitinous exoskeleton that is less easily digested than soft-bodied insects (Borror et al. 1976). The extent of the occurrence of a gastric chitinolytic system in birds is unknown (see Jeuniaux 1961), but it has been found in most of the few species studied (Ziswiler and Farner 1972). It is probably reasonable to assume that not all of the protein of a hard-bodied insect is digestible by nestlings. Thus, the difference in the total digestible protein brought per half hour to broods of four and five 8-day-old young is probably smaller than the difference between the values calculated in Table 4.

The similarity in growth rates of the young in the three brood sizes (Fig. 3) indicates that differences in feeding rates and food items fed do not affect the growth of the young. Thus, the larger number of insects brought by parents with four young may have been of lower quality, as suggested, or, alternatively, the young in broods of four may have been overfed, in that they may not have been able to assimilate all the nutrients from their food. Overfeeding in birds has never been reported, however, and would be contrary to expectations of optimal parental behavior.

ACKNOWLEDGMENTS

We thank Dr. J. M. Shay and the staff of the University of Manitoba Field Station (Delta Marsh) for providing pleasant surroundings and help during our field studies. The Portage Country Club kindly permitted us to conduct part of this work on their property. B. D. J. Batt, L. B. Best, T. D. Galloway, H. B. Tordoff, T. J. Wiens, and two anonymous reviewers commented on earlier drafts of the manuscript, and their critical suggestions were valuable. We extend our appreciation to H. den Hann, J. L. Morgan, J. M. Porter, and G. D. Sutherland, who assisted in aspects of the field work. T. D. Galloway kindly identified and confirmed our identifications of the arthropods from the stomach samples. D. Waddell, Manitoba Department of Agriculture, arranged for the analysis of the protein content of the insect food, for which we are grateful.

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada (A9556) and the University of Manitoba Research Board to Sealy. Biermann received personal support from a University of Manitoba Fellowship for 1979–1980. This paper is contribution number 70 of the University of Manitoba Field Station (Delta Marsh).

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