# FEEDING OF NESTLING AND FLEDGLING EASTERN BLUEBIRDS

BENEDICT C. PINKOWSKI

Several workers (Forbes 1903, Beal 1915, Cottam and Knappen 1939, Davison 1962) have described the prey consumed by adult Eastern Bluebirds (*Sialia sialis*). No definitive studies, however, have been done on the diet of nestling and fledgling bluebirds. In this paper I summarize the behavior of Eastern Bluebirds feeding young, describe the diet of nestling and fledgling bluebirds, and discuss the relationship between the foraging tactics of bluebirds (Goldman 1975, Pinkowski 1977) and types of prey fed to the young.

## METHODS

Observations were made of Eastern Bluebirds nesting in nest boxes in Macomb Co., Michigan from 1971 to 1973. Nest sites were located in old fields adjacent to oak (*Quercus* sp.) woodlands. Details of the study area are published elsewhere (Pinkowski 1975, 1976a). Relevant aspects of bluebird foraging were dealt with in a companion paper (Pinkowski 1977).

I sampled 2503 nestling foods at 45 nests in 20 different nest sites and 275 fledgling foods for 12 different broods. Animal foods were grouped into 23 taxonomic categories (often families, occasionally orders or genera). I note individual prey species if these appeared important and follow Cantrall (1968) and Kaston (1948) in assigning names of various Orthopterans and spiders, respectively.

Nestling diet was sampled in part by using throat collars made from pipe-cleaners or heavy thread to prevent the young from swallowing food. The collars did not appear to harm the nestlings. Nests being sampled were checked every 20 to 30 min and young were not deprived of food for more than 1.5 to 2.5 h per day. Rarely was the same nest sampled on 2 consecutive days. Throat collars were difficult to use on small, recently-hatched young unless an assistant held the bird while a collar was being applied.

The use of throat collars may generate results biased in favor of large items because smaller items are likely to slip past the neck band (Orians 1966). To offset this bias and enlarge the sample, I used 2 other methods of sampling foods: observations with a spotting scope (15–60×) and salvaging specimens (or portions thereof) from the nest cavity or from the crops of dead nestlings. Salvaged specimens included food dropped by the adults on trips to the nest and yielded small food items not likely to be obtained by other methods. I found observing nests with a spotting scope useful on older nestlings that could not be disturbed because of the possibility of premature fledging. This technique also permitted me to obtain a sample of 1359 foods fed by adults of known sex (bluebirds are sexually dichromatic), and it was the only procedure used to sample the food of fledglings. My presence 10–20 m from the nest did not disturb adult birds feeding nestlings or fledglings. Altogether, 54.3% of the nestling food data was obtained by using a spotting scope, 36.9% by using throat collars, and 8.8% by salvaging specimens.

I sampled foods evenly throughout the day and nestling period to make the data as representative of the diet as possible. Observations were conducted randomly to limit interactions among variables. For example, nestlings of a given age were observed at different times of day to minimize the effects of diurnal variations in diet and feeding rate.

Food items fed to the young are summarized as the percent occurrence of the various taxonomic groups. Diurnal variation in prey and feeding rate was studied by assigning activities to 1 of 4 time periods: early morning (06:00–10:00 EST), late morning (10:00–13:00), afternoon (13:00–16:00), and early evening (16:00–20:00); 28.9%, 32.3%, 20.7%, and 18.1% of the nestling diet was sampled during the 4 time periods, respectively. Food sampling activity was proportionate to the number of active nests and extended from 9 May to 15 August. Young of most first (spring) broods hatch in mid-May and fledge in early June; second (summer) broods fledge between mid-July and mid-August (Pinkowski 1976b). Nestling food samples were obtained on a monthly basis as follows: May, 41.5%; June, 22.5%; July, 25.8%; and August, 10.3%. Sampling was done under all types of weather conditions, but results are slightly biased in favor of insects fed during non-rainy conditions.

Vegetable matter is sporadic in the diet of nestlings and plant specimens found in the nest cavity were not necessarily fed to the young because the brooding parent may regurgitate fruit seeds and skins (pers. obs.). For these reasons I analyzed the plant and animal portions of the nestling diet separately. I included fruit in tabulations of the fledgling diet because the limitations do not apply to young out of the nest.

Distances that adults foraged from the nest were recorded at 2 nests containing 3 and 5 young during the final week of the nestling period. Markers were placed in several directions at known intervals from the nest. Foraging bluebirds travel great distances and at least 2 (often 3) observers communicating by radio were required to follow the birds and determine distances and directions at which prey was obtained relative to the nest. Directions were placed in 1 of 16 categories (N, NNW, NW, etc.) for analysis of directional overlap by foraging adults.

Feeding rates are expressed in feedings per young per 15 h (= 1 day) and represent the average of results obtained for individual observation periods lasting 1–2 h ($\bar{x} = 86.5$ min). I considered 1 trip to the nest with food as a single feeding regardless of the number or size of the prey. The male bluebird, like males of some other passerines, may offer food to the brooding female who in turn delivers it to the young. At some nests 70–90% of the nestlings' food on the day of hatching is fed to them in this way. I considered food transfers, which become less common during the first week and are rare thereafter, as male feedings although the food is actually fed to the young by the female.

Frequency data, including the number of feedings of the male relative to the female, were examined for significant differences by Chi-square. Differences in absolute feeding rates (feedings/young/day) were tested by a one-way analysis of variance and Duncan's multiple range test (Steel and Torrie 1960:107). Diversity indices for prey taxa ($H = -\sum_i p_i \ln p_i$, where $p_i$ is the proportion of prey in the $i^{th}$ taxon) were calculated from information theory (Shannon and Weaver 1949). Because the diversity index is sensitive to sample size (Orians 1966, Pielou 1966) which in turn affects the number of prey categories, I use this index only to compare groups having similar sample sizes.

## RESULTS AND DISCUSSION

*Rate of feeding nestlings.*—Female bluebirds offered proportionately more feedings to nestlings (54.8%) than males (45.2%). The difference is significant ($\chi^2 = 19.0$, $P < 0.01$, N = 2063 feedings), but considerable variation existed from one nest to another.

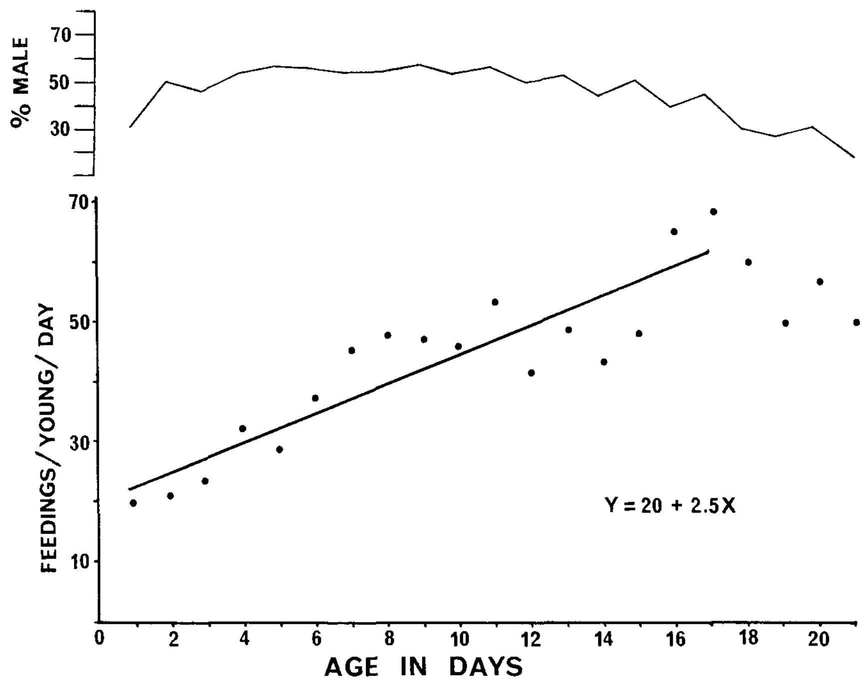


FIG. 1. Percentage of food contributed by male bluebirds and variation in feeding frequency of males and females combined during the nestling period. Data are based on 168 h of observations (minimum: 5 h/nestling age). The line shows the significant linear regression ($P < 0.05$) that existed for the first 17 days.

Feeding rate of both males and females did not depend on brood size. Males averaged 6.4, 4.8, and 5.5 feedings/h to nests containing 3, 4, and 5 young, respectively. Corresponding figures for females are 6.5, 6.5, and 6.4 feedings/h. Consequently, young in nests containing 5 young received fewer feedings/day (35.5) than those in nests containing 4 young (42.2) or 3 young (64.3). That feeding rate did not increase with brood size may in part reflect a reduction in heat loss because of more insulation and less surface exposure in larger broods (Mertens 1969).

Bluebirds increased the feeding rate with nestling age during the first 17 days of the nestling period (Fig. 1). During the first few days after hatching there was an increase in prey size, and late in the nestling period adults occasionally brought more than one item per trip to the nest. These changes tended to offset the increase in feeding rate with nestling age.

The male and female contributed nearly equal proportions of the nestlings' food during the first 5 days of the nestling period (Fig. 1). Thereafter, the

Table 1
DIURNAL VARIATION IN FEEDING RATE OF EASTERN BLUEBIRDS IN SOUTHEASTERN MICHIGAN, 1971–1973

| | No. Feedings | |
|---|---|---|
| | Male | Female |
| Early Morning | 224 (37.6%) | 371 (62.4%) |
| Late Morning | 281 (46.2%) | 327 (53.8%) |
| Afternoon | 202 (47.1%) | 227 (52.9%) |
| Early Evening | 225 (52.2%) | 206 (47.8%) |

female ceased brooding during the day (Pinkowski 1975) and continued to increase her feeding rate until day 16; after day 16 the female feeding rate remained relatively constant (35.2–41.8 feedings/young/day; $\bar{x} = 38.5$). The male feeding rate (feedings/young/day) was low on days 1–5 ($\bar{x} = 13.0$), was significantly greater ($\bar{x} = 24.8$, $P < 0.001$) and fairly constant (range = 17.6–28.8) on days 6–17, and significantly decreased ($\bar{x} = 14.9$; $P < 0.01$) on days 18–21. Thus the overall increase in the feeding rate was at first attributable to an increase in the feeding rate of both adults and later was due to an increased rate by the female only. The decrease in the feeding rate late in the nestling period was largely attributable to a reduction in feeding by the male.

Some male bluebirds ceased feeding the young soon after fledging. On 3 occasions males began new nests with different mates before young of the previous nest were independent, a behavior not observed among females. In such instances the female continued to feed the brood and supplied all of its nutritional requirements.

Feeding rate (feedings/young/day) of males and females combined was greatest in early morning (49.2), lowest in the afternoon (39.9), and nearly identical in late morning and early evening (45.3 and 45.8, respectively). Although none of the differences in feeding rates for the 4 time periods is significant ($P > 0.5$), proportionately more feedings observed in the early morning period (Table 1) were made by the female ($\chi^2 = 35.8$, $P < 0.001$). Also, males fed more and females fed less during the successive time periods; the trend was significant ($Z = 4.6$, $P < 0.001$; Snedecor and Cochran 1967: 246). Thus there was a division of the daily "work load" by males and females that may function to keep the number of feedings to the young relatively constant throughout the day.

## FOOD FED TO NESTLINGS

*Summary of invertebrate prey.*—Lepidopterous larvae comprised the largest percentage (32.4%) of animal food noted in the nestling diet and consisted of several families, including Noctuidae ("cutworms"), Arctiidae, Pieridae, Geometridae, Notodontidae, Pyralidae, and Sphingidae. Adult Lepidoptera accounted for 3.6% of all animal foods recorded and consisted entirely of moths (Heterocera).

Orthopterans were the second largest group represented (25.6%), and included grasshoppers (Acrididae and one Tetrigidae), 12.8%; crickets (Gryllidae, mostly the spring field cricket, *Gryllus veletis*; Alexander and Bigelow 1960), 9.3%; shield-bearing katydids (Tettigoniidae: Decticinae; *Atlanticus testaceus*), 1.6%; various other katydids (Tettigoniidae exclusive of Decticinae) such as *Neoconocephalus* sp., *Amblycorypha* sp., and *Pterophylla* sp., 1.5%; and mantids (Mantidae, all nymphs), 0.4%. Spiders (Arachnida: Araneae, including egg sacs, and a few Phalangida) were the third largest group (11.3%), and generally consisted of wandering, ground-dwelling species such as *Lycosa frondicola.*

Other taxa less frequent in the nestling diet were beetles (Coleoptera; mostly *Phyllophaga* sp., *Melanotus* sp., *Scarites* sp., and *Cicindela* sp. adults, and Carabidae and Elateridae larvae), 11.0%; earthworms (Annelida: Oligochaeta; *Lumbricus* sp.), 5.2%; various Hymenoptera (mostly carpenter ants, *Camponotus* sp., and some Ichneumonidae), 3.9%; and millipedes (Diplopoda), 2.3%.

Food items uncommon in the nestling diet were: leafhoppers (Homoptera: Cercopidae and Cicadellidae), 1.5%; sowbugs (Isopoda), 0.8%; snails and snail shells (Pulmonata), 1.2%; flies (Diptera), 0.5%; scorpion-flies (Mecoptera), 0.3%; dragonflies (Odonata: Anisoptera), 0.1%; *Cicada*, 0.1%; large bugs (Hemiptera), 0.1%; and lacewings (Neuroptera: Chrysopida), 0.04%. Unusual prey were 2 centipedes (Chilopoda, 0.1%) and 1 fairy shrimp (Anostraca, 0.04%).

*Variations attributable to nestling age.*—Spiders and Lepidoptera larvae were the primary food of recent hatchlings (Table 2). As the young mature more Orthoptera (Gryllidae and Acrididae), Coleoptera, and earthworms were fed. Prey diversity was lower early in the nestling period ($H = 1.60$ for young 1–5 days old) than later ($H = 2.05$ and 2.04 for young 6–10 and 11–18 days old, respectively).

Nine of 12 food items fed to young 1 day old or less were spiders. Twelve spider species were noted only once during the sampling period; 9 of these species occurred only in the diet of nestlings 4 days old or less. Other passerines also exhibit a preference to feed spiders to recent hatchlings (Royama 1970). Small nestlings must be fed small, easily digested foods, and prey with a high energy content relative to its size would seem most desirable. Spiders have a soft abdomen, lack coarse appendages, and have greater caloric

Table 2

Frequency of Animal Foods Fed to Nestling Eastern Bluebirds in Southeastern Michigan, 1971–1973

| | 0–5 Days Old | | 6–10 Days Old | | 11–18 Days Old | |
|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % |
| Lepidoptera larvae | 163 | 41.6 | 192 | 35.0 | 402 | 39.1 |
| Arachnida | 121 | 30.9 | 63 | 11.5 | 70 | 6.8 |
| Acrididae | 27 | 6.9 | 86 | 15.7 | 171 | 16.6 |
| Gryllidae | 29 | 7.4 | 56 | 10.2 | 86 | 8.4 |
| Coleoptera | 4 | 1.0 | 28 | 5.1 | 48 | 4.7 |
| Heterocera adults | 26 | 6.6 | 33 | 6.0 | 31 | 3.0 |
| Hymenoptera | 4 | 1.0 | 40 | 7.3 | 50 | 4.9 |
| *Lumbricus* sp. | 4 | 1.0 | 12 | 2.2 | 81 | 7.9 |
| *Atlanticus testaceus* | 3 | 0.8 | 13 | 2.4 | 21 | 2.0 |
| Tettigoniidae | 2 | 0.5 | 3 | 0.5 | 25 | 2.4 |

equivalents than Acridids and earthworms (cal/g dry wt; Golley 1961, Van Hook 1971) that bluebirds feed more often to older nestlings.

Large spiders (e.g., *Lycosa frondicola* and *Schizocosa avida*) were noted in the diet of older nestlings, and male and female spiders of dimorphic species were selected by size for young of different ages. Eleven *L. frondicola* males were fed to nestlings averaging 5.8 days old, whereas 7 females of this species (which are larger than males) were fed to young an average of 7.1 days old. A similar trend appears among some Orthoptera; nymphs of the grasshopper *Melanoplus bivittatus* were fed to 3-day-old nestlings and the coarser adults were not fed until day 7 (males, which are smaller than females) and day 9 (females).

*Variations attributable to season.*—Invertebrate prey fed to nestlings and tabulated on a monthly basis revealed that spiders were fed more in May and June (13.1% and 14.3%, respectively) than July (7.9%) and August (4.4%). The seasonal decline in frequency of spiders was not entirely attributable to a decrease in availability. *L. frondicola* and *Phidippus princeps*, the most common spiders in the nestling diet in spring, were not fed after early June (Fig. 2) although both species are present from April to October at the latitude of my study area (Dondale 1971).

Ground-dwelling spiders belonging to the family Lycosidae (e.g., *L. frondicola*, *Trochosa terricola*) were more common in the diet of nestlings in spring. In summer, however, spiders of the family Thomisidae (e.g., *Tibellus oblongus*, *Xysticus elegans*) that dwell on herbaceous plants and tree trunks (Lowrie 1948) were more common. The Lycosid *Schizocosa avida*

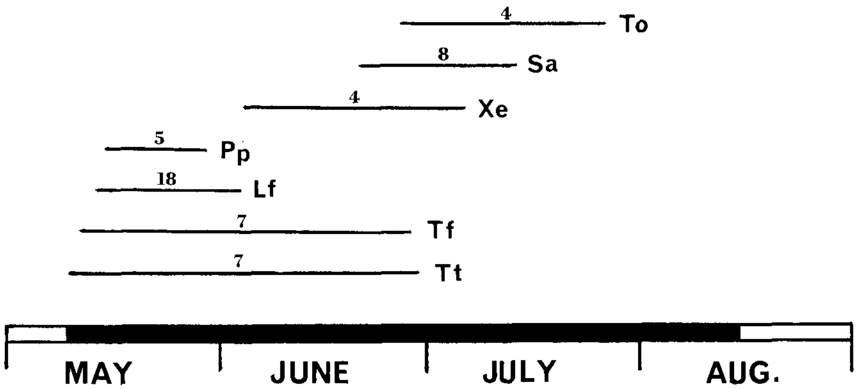


FIG. 2. Seasonal variation of spider taxa in the diet of nestling bluebirds. Numerals indicate sample sizes. All taxa noted at least 3 times are included. The solid portion of the time scale indicates the sampling period. The species are represented as follows: *Trochosa terricola* (Tt), *Thanatus formicinus* (Tf), *Lycosa frondicola* (Lf), *Phidippus princeps* (Pp), *Xysticus elegans* (Xe), *Schizocosa avida* (Sa), and *Tibellus oblongus* (To).

is common in summer but this species, like the Thomisids and unlike the other Lycosids, is phytophilous (Kuenzler 1958).

Lepidoptera adults (all moths) were more common in the nestling diet in summer (5.6%) than in spring (2.9%). Earthworms and Coleoptera were staple food items in spring, especially during rainy periods, but became less important later in the season. Earthworms comprised 10.8% of the nestling diet in May and 3.3% in June, but were absent after 1 July. Coleoptera comprised 17.9% of the diet in May, 8.3% in June, 5.9% in July, and 0.8% in August. Hymenoptera were more common in May (4.7%) and June (4.8%), when swarming carpenter ants were frequently taken, and less common in July (2.6%) and August (2.4%).

Lepidoptera larvae were more common in the diet during May (35.4%) and June (41.8%) than July (20.8%) and August (28.9%). As was the case for spiders, seasonal changes in occurrence of larval Lepidoptera reflected changes in availability, but geophilous forms were more common early in the season. Cutworms (Noctuidae larvae) accounted for 46.6% (N = 393) of all Lepidoptera larvae noted in the diet. One species, the bronzed cutworm (*Nephelodes minians*), comprised 48.6% of the cutworms recorded and is typical of the prey belonging to this taxon in that it feeds at night but is found on the ground during the day. The percentage of cutworms among all Lepidoptera larvae fed to nestlings was greatest in May (74.6%, N = 134) and decreased in June (36.4%, N = 140), July (33.7%, N = 83), and August

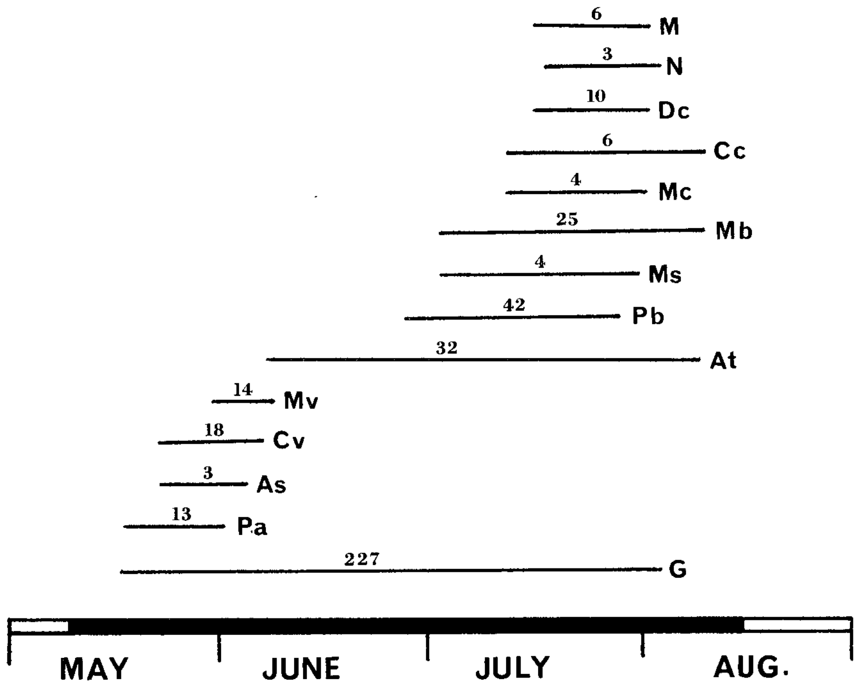


FIG. 3. Seasonal variation of Orthoptera taxa in the diet of nestling bluebirds. Numerals indicate sample sizes. All taxa noted at least 3 times are included. The solid portion of the time scale indicates the sampling period. Individual species and genera are represented as follows: *Gryllus* sp. (G), *Pardalophora apiculata* (Pa), *Arphia sulphurea* (As), *Chortophaga viridifasciata* (Cv), *Melanoplus viridipes* (Mv), *Atlanticus testaceus* (At), *Pseudopomala brachyptera* (Pb), *Melanoplus sanguinipes* (Ms), *Melanoplus bivittatus* (Mb), *Melanoplus confusus* (Mc), *Chorthippus curtipennis* (Cc), *Dissosteira carolina* (Dc), *Neoconocephalus* sp. (N), and *Mantis* sp. (M).

(11.4%, N = 35). Larvae of other Lepidoptera families (e.g., Geometridae) that inhabit trees and vegetation became increasingly common as the season progressed, but maximum consumption of all families combined occurred in June.

Orthoptera were more common in the diet in summer than spring, although individual species recorded were dependent on season (Fig. 3). *Gryllus veletis*, the most common Orthoptera noted, increased steadily from May through July (5.1%, 8.4%, and 17.6% for the 3 months, respectively). *G. veletis* nymphs were fed in mid-May, adults in late May, and peak predation occurred in mid-July. Acrididae increased steadily from May to August (5.5%, 9.2%, 23.4%, and 26.9% for each month, respectively).

The incidence of various Orthoptera in the nestling diet differed little from the chronological appearance of the various species in the study area (pers. obs.; Cantrall 1968). Orthopteran species of similar size and habits, however, complemented each other in the diet on a seasonal basis. In summer adults of *Atlanticus testaceus*, a large, geophilous species, replaced *G. veletis* in the diet. Large vernal Acridids that overwinter as nymphs in southern Michigan (*Chortophaga viridifasciata* and *Pardalophora apiculata*) were replaced in summer by other large Acridids (*Dissosteira carolina, Melanoplus bivittatus*). Similarly, the smaller Acridids *Arphia sulphurea* and *Melanoplus viridipes* were common in spring and were replaced in summer by *Pseudopomala brachyptera, Chorthippus curtipennis, Melanoplus confusus*, and *M. sanguinipes*, which are also small.

Phytophilous Orthoptera (*Neoconocephalus* sp. and *Mantis* sp.) were fed to nestlings only in summer. Thus for all 3 of the major prey groups (Lepidoptera larvae, Arachnids, and Orthoptera), bluebirds tended to select geophilous species in spring and phytophilous species in summer. Phytophilous invertebrates were undoubtedly more abundant relative to geophilous taxa late in the season as vegetation height increased, but in some cases geophilous prey were present late in the season, but were ignored by bluebirds.

Evans (1964) found that Vesper Sparrows (*Pooecetes gramineus*), Song Sparrows (*Melospiza melodia*), and Chipping Sparrows (*Spizella passerina*) breeding in southern Michigan use a greater variety of food in summer than spring. I found this somewhat true of bluebirds; 19 of the 23 (82.6%) prey categories were represented during July whereas only 14 (60.9%) were recorded in May. Diversity indices were higher in July (2.24) and August (2.09) than in May (1.95) and June (1.96).

*Variations attributable to time of day.*—Several classes of prey, including Arachnida, Coleoptera, Heterocera, and Tettigoniidae, displayed no frequency variation with time of day; others, however, were more variable. Gryllidae were fed more in early morning (13.7%) and early evening (13.5%) than late morning (4.9%) and afternoon (4.2%). Acrididae displayed the reverse pattern (19.0% in the afternoon, 18.7% in the late morning, 12.8% in early evening, and 8.0% in early morning). Thus both Gryllidae and Acrididae were apparently preyed upon most often when they were most active.

Lepidoptera larvae were abundant (39.2–44.7%) from early morning until late afternoon and less common (29.2%) in early evening. Hymenoptera were most abundant in early evening (8.3%) when bluebirds frequently engage in flycatching (Pinkowski 1977); they were least common in the afternoon (0.6%) and intermediate (4–5%) in the other periods. Earthworms were most common in early evening (8.7%) and afternoon (7.3%), and less common (1.6–3.0%) in other periods.

Prey diversity was greatest in early evening (H = 2.18), partly because aerial insects (Hymenoptera, Diptera) were added to the diet at that time. Diversity was lowest in the afternoon (H = 1.72) when feeding rate was reduced, and was greater in late morning (H = 1.93) and early morning (H = 1.90).

Small stones, snails, and snail shells function as grit (Royama 1970) and were noted only in the early morning. The female bluebird apparently supplies nearly all of the grit required by nestlings. Seven observed feedings of grit were all made by the female.

*Variations attributable to weather.*—Precipitation (mostly rainfall except during March) increased during the 3 years of study; 15.3 cm of precipitation fell from 1 March to 30 June 1971, and 25.6 cm and 38.6 cm were recorded for the same period in 1972 and 1973, respectively. Annual incidence of Acrididae in the diet decreased with the increasing precipitation (20.1%, 16.1%, and 4.7% for the 3 consecutive years); the same trend occurred among Gryllidae (17.1%, 8.5%, and 4.9%). Some Orthoptera, especially grasshoppers, flourish during periods of drought and are reduced in numbers during rainy years (Shelford 1963:318, Scharff 1954).

More earthworms were taken in 1973 (14.0%) than in 1971 (2.9%) and 1972 (1.5%). A paucity of Lepidoptera larvae in the diet in 1971 (19.9%) compared with 1973 (35.7%) and 1972 (38.2%) may have been attributable to death of these insects from desiccation during dry conditions (Andrewartha and Birch 1960) or other factors such as lack of food. In any event, bluebirds tend to feed Orthoptera during dry seasons and Lepidoptera larvae and earthworms during rainy seasons, presumably because of differences in relative availability.

*Fruit fed to nestlings.*—Vegetable matter, uncommon in the diet of nestlings, was noted at only 4 of 45 nests observed. The fruits involved were mulberries (*Morus* sp.), raspberries (*Rubus* sp.), dogwood (*Cornus stolonifera*), cherry (*Prunus virginiana*), and honeysuckle (*Lonicera* sp.). Fruit was not fed before late June, when it became abundant in the study area. At 2 of the 4 nests, each containing nestlings within a few days of fledging, fruit comprised 33.0% and 37.0% of the nestling diet over 3 and 5 day periods, respectively (approximately 15 h observation in each case). At the 2 other nests fruit was noted only once; each instance involved older nestlings ($\geqslant$14 days old).

Morton (1973) concluded that a fruit diet prolongs nestling development and is selected against as a food for poikilothermic young on account of its low protein content. The altricial strategy, he argues, requires that the small young be able to use food principally for growth and not for heat production (because the nestlings' heat requirements are satisfied by brooding). Fruit, therefore, is not a dietary constituent of young bluebirds until the last week of the nestling period, when the nestlings are completely endothermic (Pinkowski 1975).

*Partitioning of the feeding niche.*—A foraging pair of adult birds may reduce competition by differentially using the feeding resources available to them without necessarily involving secondary sexual dimorphism (Ligon 1968, Jackson 1970). I noted no difference in the diversity of foods fed to the young by male (H = 1.89) and female (H = 1.87) bluebirds. Males, however, fed significantly more Gryllidae ($\chi^2$ = 4.9, $P < 0.05$) and earthworms ($\chi^2$ = 21.9, $P < 0.001$) than females; females fed more Acrididae ($\chi^2$ = 5.4, $P < 0.05$), Hymenoptera ($\chi^2$ = 4.2, $P < 0.05$), and Arachnida ($\chi^2$ = 4.9, $P < 0.05$) than males. Little difference was noted among other prey categories including moths ($\chi^2$ = 0.8, $P > 0.3$) and Lepidoptera larvae ($P > 0.9$).

I could not attribute differences in foods fed by males and females to different feeding rates of males and females relative to age of the nestlings. Earthworms and crickets, preferred foods of males, were most common in the diet of older nestlings that were fed more by females. Spiders were relatively uncommon late in the nestling period when females fed more often than males. Although grasshoppers were common in the diet of older nestlings, Pinkowski (1974) noted that captive female Eastern Bluebirds and Mountain Bluebirds (*Sialia currucoides*) preferred to feed grasshoppers to nestlings.

Differential prey use may result from differential use of the feeding range by males and females. Using pooled data for 2 nests, I found that male bluebirds obtained prey for nestlings closer to the nest site ($\bar{x}$ = 113.6 m, *SD* = 99.4, N = 256) than females ($\bar{x}$ = 152.4 m, *SD* = 117.3, N = 182; t = 3.7, $P < 0.01$). Indices of overlap (Horn 1966) for directions that males and females obtained prey were great (0.875 and 0.902); apparently food resources were not partitioned on a directional basis.

In some areas male and female bluebirds forage at equal distances from the nest (Pinkowski 1974, Goldman 1975). When there is a difference in foraging distances, however, evidently the male remains closer to the nest, possibly because male bluebirds play a greater role than females in defence of the nest cavity against conspecific intruders. Females of some open-nesting species such as the Bobolink (*Dolichonyx oryzivorus*) and Henslow's Sparrow (*Ammodramus henslowii*) forage closer to the nest than males (Wiens 1969, Robins 1971).

Power (1974:88–99) related foraging distance of adults to brood size (work load) in the Mountain Bluebird. For the 2 Eastern Bluebird nests I examined, however, the adults with 3 young foraged farther from the nest ($\bar{x}$ = 166.2 m) than adults with 5 young ($\bar{x}$ = 96.2 m; t = 7.1, $P < 0.001$). Eastern Bluebirds are more dependent on feeding perches than Mountain Bluebirds and are known to vary foraging range according to perch distribution (Pinkowski 1974, 1977). Thus habitat quality appears more important than the number of young in the nest in determining how far adults travel in search of food.

### FEEDING OF FLEDGLINGS

Foods fed to fledglings differ from those fed to nestlings. Lepidopterous larvae were more common in the fledgling diet (44.0% of all fledgling foods recorded), reflecting peak consumption in June when most fledglings were out of the nest. Earthworms (11.4%) and Coleoptera (7.7%) were more common in the fledgling diet than the nestling diet, but the reverse was true for Acrididae (8.8%), Arachnida (4.4%), Gryllidae (3.3%), and Heterocera (3.3%). Fruit (mulberries and cherries) comprised 11.0% of the fledgling diet, but was noted only during the summer period (July and August). General observations indicated that the adults feed smaller items to fledglings than nestlings.

Feeding patterns of adults foraging for fledglings differ from those of adults feeding nestlings. Fledgling bluebirds spend most of their time in large trees and alternate active and inactive periods; they begin calling when hungry and, depending on food availability, receive several feedings until satiated. Adults obtain many food items within a few meters of the fledglings, often by gleaning from the tree tops, and many small items may be fed in rapid succession to young out of the nest. This is in contrast to the long trips with large items made regularly by adults with young in the nest.

### CONCLUSIONS

Prey availability is important in determining dietary constituents of young bluebirds. Weather and time of day influence prey activity and abundance and hence affect what is fed to the young. The presence of smaller nestlings somewhat restricts prey selection because older young are fed a greater variety of foods. As the spectrum of suitable prey increases with nestling age, however, so does the amount of food required by the young and consequently the feeding rate of adults. These changes would tend to equalize the time and energy expended by adults during the duration of the nestling period.

The data obtained in this study corroborate Goldman's (1975) conclusion that bluebirds feed large food items to nestlings. Lepidoptera larvae (especially cutworms) are the preferred food for nestlings. Beal (1915), however, states that Orthoptera are preferred by adult bluebirds and noted that Coleoptera are nearly twice as common in the diet of adults (29.9%) as I found in the diet of nestlings. Although Orthoptera and Coleoptera are large, their relative infrequency in the diet of the young may be explained by their coarseness.

Coarse foods require more preparation and thereby reduce caloric yield per unit time, the basic determinant of food value (Emlen 1966).

Foraging bluebirds locate prey from a distance by using conspicuous feeding perches; in spring most prey is obtained after a short "drop" to the ground, but in summer there is an increased use of tactics such as gleaning and flycatching that result in prey capture above ground (Pinkowski 1977). Analysis of seasonal variation in prey taxa suggests that the seasonal trend in foraging tactics is independently related to both a seasonal increase in vegetation biomass (height and density) and an increase in the abundance of invertebrates living above ground. Bluebirds rarely feed by dropping onto the ground in areas having tall, dense vegetation, probably because doing so would often require them to relocate prey from close range and not from a conspicuous and elevated position (Pinkowski 1974:66). Thus late in the season bluebirds do not feed upon some geophilous prey taxa (earthworms, cutworms, Coleoptera, and some spiders) that are still available, but instead exploit phytophilous and aerial prey (moths and certain spiders, Lepidoptera larvae, and Orthoptera) that are more abundant and conspicuous from a distance than geophilous prey. By changing their predatory tactics on a seasonal basis, bluebirds are able to exploit changes in prey availability as well as maintain the optimum predatory efficiency permitted by their perch-feeding habit.

## SUMMARY

The behavior of adult Eastern Bluebirds feeding nestlings and fledglings and the diet of young bluebirds were studied in southeastern Michigan from 1971 to 1973. Females fed nestlings more often than males. The feeding frequency increased with nestling age until just prior to fledging, when a decline occurred. Feeding rate of males and females combined was relatively constant throughout the day although females fed young more often earlier in the day and male feeding rate was greater later in the day.

Lepidoptera larvae were the most common food of both nestlings and fledglings and comprised 32.4% of the nestling diet. Orthoptera (mostly Acrididae and Gryllidae) were also common (25.6%), especially in summer. Spiders (11.3%) were particularly important early in the season and for newly-hatched young. Fruit was uncommon in the diet of nestlings but was fed to fledglings in summer and made up 11.0% of all fledgling foods recorded.

Adult males and females fed different foods to the young, thereby partitioning the feeding niche. Males fed significantly larger percentages of Gryllidae and earthworms; females fed larger percentages of Arachnida and Acrididae.

## ACKNOWLEDGMENTS

Portions of this paper originally comprised part of a Ph.D. dissertation submitted to the Department of Biology, Wayne State University. William Thompson, Claude Rogers, Melvin Weisbart, Stanley Gangwere, and Diane Pick read the manuscript and made helpful suggestions and criticisms. Charles Dondale identified the spiders, and Michael Tyrkus, John Newman, and Eric Quinter helped identify many of the insects. James

Stevens, Patrick Pinkowski, and my wife, Phyllis, gave unselfish assistance in the field. I am grateful for the help of all these persons.

## LITERATURE CITED

ALEXANDER, R. D. AND R. S. BIGELOW. 1960. Allochronic speciation in field crickets, and a new species, *Acheta veletis*. Evolution 14:334–346.

ANDREWARTHA, H. G. AND L. C. BIRCH. 1960. Some recent contributions to the study of the distribution and abundance of insects. Annu. Rev. Entomol. 5:219–242.

BEAL, F. E. L. 1915. Food habits of the thrushes of the United States. U.S.D.A. Biol. Surv. Bull. 280.

CANTRALL, I. J. 1968. An annotated list of the Dermaptera, Dictyoptera, Phasmatoptera, and Orthoptera of Michigan. Mich. Entomol. 1:299–346.

COTTAM, C. AND P. KNAPPEN. 1939. Food of some uncommon North American birds. Auk 56:138–169.

DAVISON, V. E. 1962. What bluebirds eat. Aud. Mag. 64:223–224.

DONDALE, C. D. 1971. Spiders of Heasman's field, a mown meadow near Belleville, Ontario. Proc. Entomol. Soc. Ontario 101:62–69.

EMLEN, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611–617.

EVANS, F. C. 1964. The food of Vesper, Field, and Chipping sparrows nesting in an abandoned field in southeastern Michigan. Am. Midl. Nat. 72:57–75.

FORBES, S. A. 1903. On the food of birds. Bull. Ill. Lab. Nat. Hist. 1:86–162.

GOLDMAN, P. 1975. Hunting behavior of Eastern Bluebirds. Auk 92:798–801.

GOLLEY, F. B. 1961. Energy values of ecological materials. Ecology 42:581–584.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419–424.

JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. Ecology 51:318–323.

KASTON, B. J. 1948. Spiders of Connecticut. Conn. State Geol. Nat. Hist. Surv. Bull. 70:1–874.

KUENZLER, E. L. 1958. Niche relations of three species of lycosid spiders. Ecology 39:494–500.

LIGON, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85:203–215.

LOWRIE, D. C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29:334–351.

MERTENS, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits, *Parus major major*. Ibis 111:11–16.

MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Am. Nat. 107:8–22.

ORIANS, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321–337.

PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13:131–144.

PINKOWSKI, B. C. 1974. A comparative study of the behavioral and breeding ecology of the Eastern Bluebird (*Sialia sialis*). Ph.D. thesis, Wayne State Univ., Detroit, Mich.

———. 1975. Growth and development of Eastern Bluebirds. Bird-Banding 46:273–289.

———. 1976a. Use of tree cavities by nesting Eastern Bluebirds. J. Wildl. Manage. 40:556–563.

———. 1976b. Photoperiodic effects on the postjuvenal molt of the Eastern Bluebird. Ohio J. Sci. 76:268–273.

———. 1977. Foraging behavior of the Eastern Bluebird. Wilson Bull. 89: 404–414.

POWER, H. W. 1974. The Mountain Bluebird: sex and the evolution of foraging behavior. Ph.D. thesis, Univ. Mich., Ann Arbor, Mich.

ROBINS, J. D. 1971. Differential niche utilization in a grassland sparrow. Ecology 52: 1065–1070.

ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (*Parus major* L.). J. Anim. Ecol. 39:619–668.

SCHARFF, D. K. 1954. The role of food plants and weather in the ecology of *Melanoplus mexicanus mexicanus* (Sauss.). J. Econ. Entomol. 47:485–489.

SHANNON, C. E. AND W. WEAVER. 1949. The mathematical theory of communication. Univ. of Ill. Press, Urbana.

SHELFORD, V. E. 1963. The ecology of North America. Univ. of Ill. Press, Urbana.

SNEDECOR, G. W. AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames.

STEEL, R. G. D. AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

VAN HOOK, R. I., JR. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecol. Monogr. 41:1–26.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1–93.

245 COUNTY LINE ROAD, BRIDGEVILLE, PA 15017. ACCEPTED 11 NOV. 1976.