# FEEDING OF NESTLING AND FLEDGLING EASTERN KINGBIRDS

ELMER L. MOREHOUSE AND RICHARD BREWER

INFORMATION on the feeding of young birds in the nest is available in varying quantity and utility for many species. The feeding of fledglings has equally important consequences to the population and the ecosystem, but information is distressingly meager. In a study of the breeding biology of the Eastern Kingbird, *Tyrannus tyrannus* (L.), it proved possible to obtain observations on the feeding of young birds during both nestling and fledgling periods.

## PROCEDURE

At nests data were gathered by direct observation through telescopes giving magnifications of 20–50×. The observer usually sat on the ground in the open. The nesting pairs showed awareness of the observer when he stood, as when arriving or leaving, but not when he was seated. Distinguishing male and female posed a problem; behavioral differences usually allowed separation of the sexes, but wherever possible we also used individual differences in appearance.

For young out of the nest, the procedures followed were these: A family group was located and observations begun if the observer's presence did not seem to disturb the birds. Observations were continued as long as any young bird could be seen. When observations were no longer possible, the observer moved carefully to bring the brood or part of it back into range. Kingbirds are a favorable species for such study, but even so the observation time as given in Table 2 represents only about half the time spent trying to make observations in the vicinity of a brood.

Dating of events in the following discussion is in relation to the hatching of the last egg during the nestling period (thus, $H+0$ = day of hatching of the last egg, $H+1$ = the next day, etc.) and in relation to the day the last young left the nest during the fledgling period (thus, $F+0$ = day the last young left the nest, $F+1$ = the next day, etc.).

Ten nests of kingbirds were located during 1959–1966 in Kalamazoo County, Michigan at the 40-acre Colony Farm Tract within the city limits of Kalamazoo and the 500-acre Fort Custer Ecological Research Area south of the Kalamazoo River near the village of Augusta. Four nests were discovered during nest building, three during incubation, and three after eggs had hatched.

One young bird was hand reared from the day it left the nest (20 July) until it was returned to the area from which it had been removed (2 August). The bird was kept outdoors (taken inside at night through 25 July) at a dwelling in a suburban neighborhood.

## BREEDING BIOLOGY

Kingbirds arrive in the vicinity of Kalamazoo about the first week in May. They take up residence in open areas with scattered trees and shrubs. The female builds the nest and lays a clutch of 2–4 eggs. Probably most pairs have begun egg laying by early June. Only the female incubates; the male usually perches near the nest during the female's inat-

TABLE 1

HOURLY RATE OF FEEDING AND PERCENTAGE OF FEEDINGS BY MALE AT SIX NESTS OF THE EASTERN KINGBIRD

| *Day* (H+) | *Hours observed* | *Feedings/nesting/hour* | | | *Percentage of feedings by male*[1] |
|---|---|---|---|---|---|
| | | *All nests* | *Broods of two* | *Broods of three* | |
| 0 | 7.2 | 0.5 | 1.0 | 0.2 | 25 |
| 1 | 3.2 | 3.0 | 9.5[2] | 1.4 | 43 |
| 2 | 6.9 | 2.1 | 1.3[2] | 2.4 | 49 |
| 3 | 14.2 | 3.4 | 2.9 | 3.5 | 54 |
| 4 | 4.4 | 2.7 | — | 2.7 | 50 |
| 5 | 2.1 | 3.1 | — | 3.1 | 63 |
| 6 | 6.2 | 3.8 | 2.8 | 2.8 (5.4[3]) | 44 |
| 7 | 3.2 | 3.0 | — | 3.0 | 57 |
| 8 | 3.5 | 5.0 | 5.0[2] | 4.9 | 49 |
| 9 | 10.2 | 5.3 | 7.6 | 3.8 | 42 |
| 10 | 15.2 | 5.4 | 6.0 | 3.5 | 49 |
| 11 | 14.2 | 6.7 | 9.1 (12.9[2,4]) | 3.8 | 42 |
| 12 | 9.0 | 5.6 | 5.5[2] | 5.9 (4.6[2,3]) | 30 |
| 13 | 4.5 | 3.9 | 3.9 | — | 69 |
| 14 | 14.2 | 5.1 | 5.5 | 4.1 | 38 |
| 15 | 16.0 | 6.2 | 4.9 (8.3[4]) | 6.4[2] | 67 |
| 16 | 7.1 | 4.9 | 5.0 (4.8[4]) | — | ? |

[1] Feedings by birds of unknown sex ignored.

[2] Sample of less than two hours.

[3] Brood of four.

[4] One young bird.

tentive periods. The incubation period is 15–16 days; hatching usually occurs in the space of a few hours in the morning. The time from hatching of the last egg until all young have left the nest is 14–17 days. Most birds have left for the south by the first week of September.

## DIET

Adult insects were the main items fed to nestlings and fledglings, just as they are the main item of the diet of adults (Beal, 1897). Dragon- and damselflies (Odonata), grasshoppers (Orthoptera), flies (Diptera), and butterflies and moths (Lepidoptera) were particularly important. Items probably secured by means other than flycatching were occasionally seen; of these, lepidopteran larvae were the most important.

Fruits made up a minor portion of the diet at most nests, but mulberries, *Morus rubra*, were fairly important at one nest. Other fruits noted were cherries, *Prunus* sp., and dewberries and raspberries, *Rubus* spp. Occasionally two fruits were brought to a nest at once; animal items were always brought singly. Fledglings beginning to forage for themselves often ate fruit and also often picked invertebrates from leaves and branches; these items are probably more important in the diet of birds at this age than at any other.

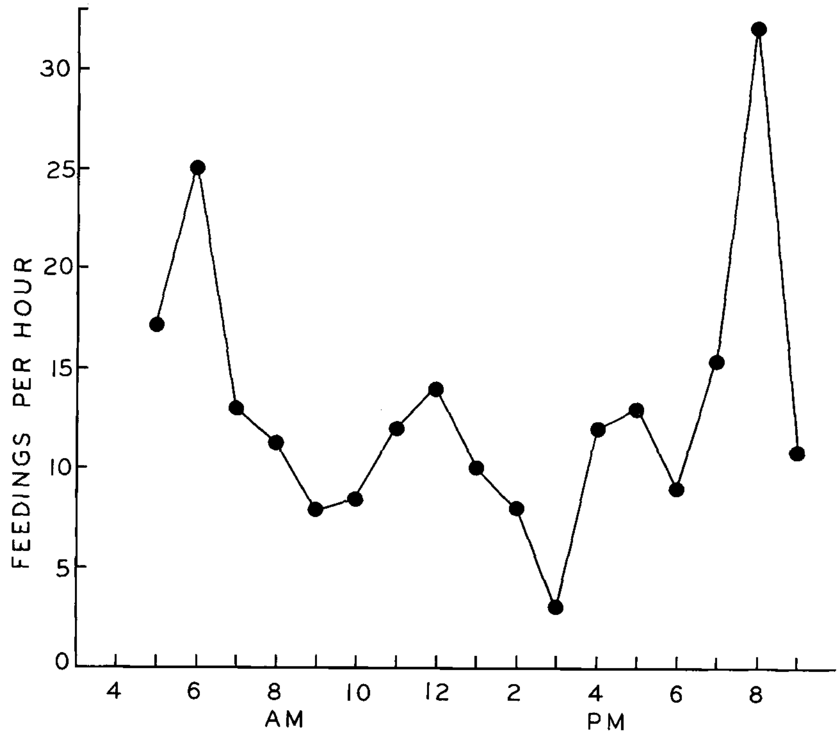


Figure 1. Hourly trend in feeding rate at Eastern Kingbird nest 3, based on 23 hours observation on days H+9–12 (5–8 July 1963). Temperature range, 17–36°C; median of hourly temperatures, 29.5. Awakening time of the female was about 5 AM; roosting time about 8:30 PM.

## FEEDING OF NESTLINGS

On the day of hatching, the feeding rate was very low, one feeding or less per young bird per hour (Table 1). The rate then rose abruptly, corresponding to an increase in feedings by the male. Through the rest of the first half of nestling life the feeding rate remained fairly constant at about three feedings per nestling per hour. Then a rise in the feeding rate corresponded with an abrupt decline in brooding by the female and an increase in the fraction of her feedings. Past this point, the pattern for two-nestling nests and three-nestling nests diverged. At nests with two young, the rate increased irregularly through the rest of nestling life. At nests with three young, the feeding rate peaked about H+9–11 at a level well above that for two-nestling broods. For the last few days of nestling life, rates were again comparable.

In what appears to be the only other quantitative study of feeding rate,

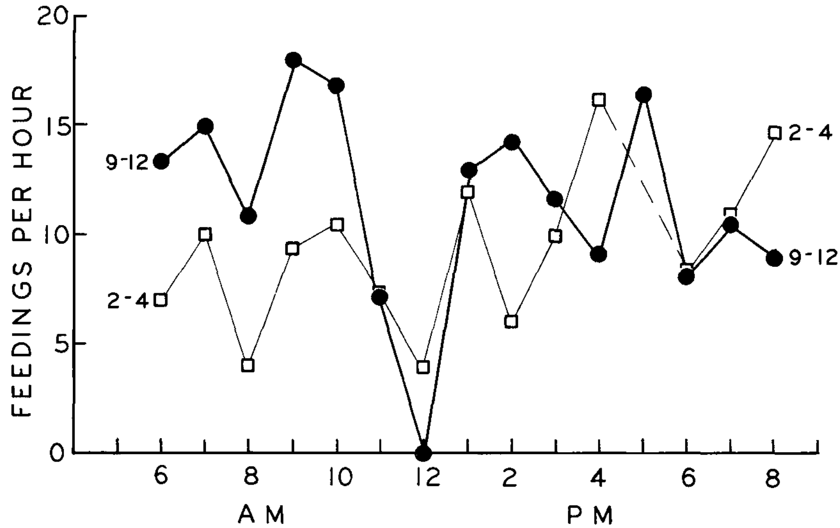


Figure 2. Hourly trend in feeding rate at Eastern Kingbird nest 4, based on 19 hours observation on days H+2–4 (14–16 June 1964; temperature range, 16–30°C; median of hourly temperatures, 20) and 21 hours observation on days H+9–12 (21–24 June 1964; temperature range, 17–32°C; median of hourly temperatures, 25). Roosting time for days 2–4 was about 8 PM; for days 9–12 about 8:20 PM. Awakening time was not determined.

Herrick (1902: 27) observed 91 feedings from 8:54 AM to 12:50 PM at a nest containing four young (two of which he had introduced a few days earlier from another nest) about 10 days old. For two young the same age, over the same span of hours, we observed 44 feedings. The rate per young bird is virtually identical.

At a given nest on a given day, the feeding rate varied with time of day, but we found no daily rhythm of feeding that could be considered characteristic of the species. Nest 3 (two nestlings) showed a striking trend in feeding activity for days 9–12: a peak early in the morning, a trough in mid-afternoon, and the day's highest rate in the hour or so before roosting when food was brought at the rate of 30 or more items an hour (Figure 1). Somewhat the same trend existed for other days at the same nest, and the evening peak was noticeable at nest 1. At nest 4 (three nestlings; Figure 2) feeding rates during days 9–12 tended to be more constant (possibly excepting an apparent drop to zero around noon; this point is based on less than an hour's observation on a single day). Good data for nest 4 are also available for H+2–4, and the pattern is reasonably similar to days 9–12 (Figure 2). For these days the feeding rate was not dependent on temperature, at least in the range from 21–33°C (thermometer 2 feet from the ground and shaded by the observer). Below 21°C feeding rates appeared somewhat higher and above 33°C, somewhat lower, but these samples are small and highly variable.

## FEEDING RATES DURING DEPARTURE FROM THE NEST

A transitional period of varying length exists when both nestlings and fledglings are being attended. We spent about 15.5 hours observing at two nests during this period. The hourly feeding rate per nestling was 6.1; for fledglings it was about 2. Difficulties in observing the fledglings make this figure subject to greater error than that for the nestlings; even if the true figure were twice the observed rate (and it certainly was not), it is still evident that the young birds in the nest remain the center of attention.

To speculate on the evolutionary value of such behavior, this period represents a particularly vulnerable time; shortening it as much as possible should be evolutionarily advantageous. Because the larger, more vigorous young usually leave the nest first, concentration of feeding on the nestlings tends to bring them up to the developmental level of the fledglings.

## FEEDING OF FLEDGLINGS

Feeding rate for the first few days out of the nest was about the same as or slightly below that of the last several days of nestling life. Apparently the peak feeding rate for the entire post-hatching period comes 8–16 days after the young have left the nest (Table 2). On F+10 the fledglings of nest 4 were fed at the rate of 10.3 feedings per young bird per hour over an observation period covering most of the forenoon (Figure 3). This is a rate almost twice as high as was observed for any substantial length of time while these young were in the nest. About three weeks post-fledging, the feeding rate declined abruptly to one feeding per fledgling per hour or less. The last feeding of young by adults was observed F+35.

Distinguishing between male and female parents was usually impossible once the young were fledged, but it was often evident that both continued to participate in feeding. No obvious differences were noted between the food items given to fledglings as compared to nestlings.

## ENERGY INTAKE

Feeding rates, although of interest in themselves, may not directly indicate energy intake of the young. This was almost certainly true for hour-to-hour comparisons of kingbirds. The sources of the discrepancy were very high and very low rates. Very high rates were for periods when feeding was concentrated close to the nest and most food items were small, readily available insects. Very low rates tended to be periods in which

TABLE 2

HOURLY RATE OF POSTFLEDGING FEEDING OF FIVE BROODS OF EASTERN KINGBIRDS

| | *Nest 4*[2] | | | *Other nests* | | |
|---|---|---|---|---|---|---|
| *Day (F+)* | *Hours observed*[1] | *Feedings observed* | *Feedings/ fledgling/ hour* | *Hours observed*[1] | *Feedings observed*[3] | *Feedings/ fledgling/ hour* |
| 0 | 1.8 | 18 | 3.4 | 1.3 | 4 (2) | 3.1 |
| | | | | 1.8 | 24 (4) | 3.4 |
| 2 | 0.5 | 8 | 4.9 | 0.3 | 5 (2) | 9.4 |
| | | | | 0.3 | 0 (3) | 0.0 |
| | | | | 0.6 | 14 (4) | 5.4 |
| 3 | 1.8 | 21 | 3.9 | 0.4 | 2 (3) | 2.2 |
| 4 | – | – | – | 0.6 | 5 (2) | 8.4 |
| | | | | 0.5 | 16 (2) | 15.0 |
| 5 | – | – | – | 0.5 | 0 (3) | 0.0 |
| 6 | 2.3 | 39 | 5.8 | 1.3 | 17 (2) | 6.4 |
| 7 | 3.9 | 49 | 4.3 | 1.0 | 12 (2) | 6.0 |
| 8 | 3.7 | 86 | 7.9 | 1.5 | 16 (2) | 5.3 |
| 9 | – | – | – | 0.2 | 2 (2) | 6.0 |
| | | | | 0.2 | 3 (4) | 4.1 |
| 10 | 2.8 | 55 | 10.3 | 2.9 | 23 (2) | 4.0 |
| | | | | 0.4 | 0 (3) | 0.0 |
| 11 | 6.6 | 69 | 5.2 | 0.7 | 9 (2) | 6.7 |
| 12 | 2.7 | 16 | 3.7 | 0.4 | 2 (3) | 2.3 |
| 13 | 2.0 | 15 | 4.6 | 0.8 | 4 (2) | 2.4 |
| 14 | 0.9 | 14 | 8.7 | 0.1 | 2 (2) | 8.2 |
| 15 | 4.9 | 53 | 6.2 | 0.6 | 1 (2) | 0.9 |
| 16 | 2.7 | 51 | 9.3 | – | – | – |
| 17 | – | – | – | 0.2 | 0 (2) | 0.0 |
| 18 | – | – | – | 0.05 | 1 (2) | 9.3 |
| 19 | 4.8 | 53 | 5.9 | – | – | – |
| 21 | 0.4 | 3 | 5.1 | – | – | – |
| 23 | 1.5 | 1 | 0.3 | – | – | – |
| 25 | 4.1 | 9 | 1.2 | – | – | – |
| 26 | 0.1 | 0 | 0.0 | – | – | – |
| 27 | 0.7 | 0 | 0.0 | – | – | – |
| 28 | 1.1 | 1 | 0.4 | – | – | – |
| 30 | 2.2 | 5 | 1.8 | – | – | – |
| 32 | 2.5 | 3 | 0.8 | – | – | – |
| 35 | 2.1 | 2 | 0.5 | – | – | – |
| 37 | 0.9 | 0 | 0.0 | – | – | – |
| 40 | 0.2 | 0 | 0.0 | – | – | – |

[1] Period when at least one young bird was under observation.

[2] Three young birds until F+23, then two.

[3] Figures in parentheses denote numbers of young being fed.

feedings, when they did occur, were of large items of (judging from dry weight) 20–30 times the caloric value of the small insects caught near the nest. We suspect that day-to-day changes in feeding rate, if based on several hours of observation per day, probably reflect changes in caloric intake fairly well. Values for later days might be underestimated if the average size of food items changed, but we believe that this was not an important consideration at the nests we studied.

We obtained an estimate of gross energy intake for the hand-reared bird

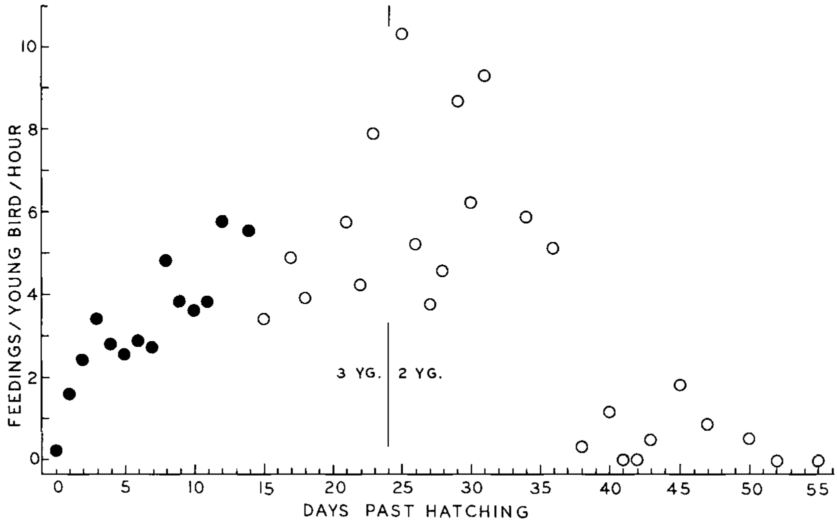


Figure 3. Feeding rate at Eastern Kingbird nest 4 from hatching until feeding of young by adults was no longer observed. Solid symbols represent feeding of nestlings; open symbols, fledglings. One fledgling disappeared about day 24. The dates run from 12 June to 6 August 1964.

for one day. On F+6 we placed an insect as nearly identical as possible to each one eaten by the bird into a jar of refrigerated water. At the end of the day this material was oven-dried at 110°C. Between 7:00 AM and 7:30 PM (air temperatures approximately 24–33°C) the bird ate insects, mostly grasshoppers, with a dry weight of 5.05 g. Using the caloric value of grasshoppers given by Golley (1961) this is a gross energy intake of about 27 Kcal. The exact weight of the bird is unknown but it was probably about 35 g (see Norris and Johnston, 1958: 116). The estimate is about what one would expect from a bird of this size under "existence" conditions (see Davis, 1955: Figure 1; West, 1960: Tables 2, 4, and 6). In fact, its energy demands must have been slightly above existence because it was still growing feathers and it took about 30 flights of 25–30 feet and about 40 flights of 2–6 feet on this day.

## Development of the Young

Shortly after hatching, the young have dark red-brown skin, whitish down, and a yellow beak with a yellow-orange gape. They lie quietly but rear up and gape when the parent arrives and also with no evident stimulus. By H+4 the skin appears blackish and a peeping call has become evident. By H+6 pinfeathers are evident; by H+7 a dark tip is beginning on the bill. By H+10 the young are kingbird-like in appearance and have heavy pinfeathers. They are active, standing up, shaking and flapping their wings. About H+11 the peeping note given previously changes to a *deek* resembling the adult's often used position note.

Leaving the nest and fledging can probably be thought of as simultaneous for kingbirds, although not until about F+2 are the young able to fly long enough to gain altitude. Even then if they fly into extensive open spaces, they tend to finish on the ground.

One young bird, six hours after it left the nest and without food in the meantime, weighed 30.02 g. This was the last bird to leave the nest and was the hand-reared bird already referred to. The tail feathers at this time were about 30 mm long. By F+11–13 the young began to resemble adults, although a number of differences still allowed easy separation of adult and young. By F+27 the main point of distinction was the tail, which was shorter and more drooping in the young.

Within a day or two after leaving the nest, the begging posture changed. The fledglings leaned forward more and did not gape so widely as nestlings, but they gave nothing like the crouching, wing-shivering display of many passerine fledglings. For the first several days the young tended to sit still for considerable periods; they did not accompany the parents on long flights, but when the adults came near the young flew toward them and begged. About F+4, a special begging call developed (we rendered it as *see-see-see-deek*!), not given by younger fledglings or nestlings.

By F+10 the young could be said to fly well, and the family group now began to range over considerably wider areas. On F+11 we noted that the young flew "on wing tips" like adults. By F+23 the young could keep up with the adults in ordinary flight, but even as late as F+30 the young tended to lose speed and altitude in the zig-zagging, acrobatic flights that one thinks of as typical of the species.

By F+7 young birds in the field were observed hopping around in trees and flying out from them, chasing insects. They were not observed to catch any until the following day. By F+7 the hand-reared bird had begun to treat live insects as adults do; it shook them and knocked them against its perch. By F+9 it tossed them into the air to arrange them headfirst. Manipulation with the tongue was prominent. In the laboratory a decrease in the amount of food taken at one feeding and an increase in frequency of desired feedings was noted about F+8. On F+10–11 both the hand-reared bird and wild birds were seen foraging on fruits. By F+10 young in the field were extremely active in obtaining food from the parents, going so far as to fly out and take food from the parent's beak in mid-air. By F+13 the young's efforts to forage for themselves were prominent. By F+26 the individual members of the family group were often seen hunting independently, but the young still tended to fly to the parents whenever the adults caught something. The begging call was still given on F+35. On F+37 and thereafter no begging calls were heard, although the young still chased adults with food. Family groups were still intact when our systematic observations ended in late August.

## TIMING OF MOLT

The molt of birds is a tangled thicket into which we venture briefly to make a point of purposely limited scope. Eastern Kingbirds, like most members of the Tyrannidae breeding in temperate America, undergo their fall molt after southward migration (Dwight, 1900: 136–140: see also Johnson, 1963). This pattern, unusual for passerines and migratory birds in general, occurs also in swallows (Dwight, 1900: 223–224). Johnson (1963: 882) pointed out that both families are "aerial-insect predators," but the correlation between this mode of foraging and the delayed molt extends beyond these families. The Meropidae show the delayed molt (Van Tyne and Berger, 1959: 92), and so also do such aerial foragers as *Caprimulgus europaeus*, *Apus apus*, and *Muscicapa striata* (Stresemann and Stresemann, 1966: 36).

For the Eastern Kingbird we offer the following hypothesis to account for its delayed molt. To begin with, we take it as a commonplace that molt occurs when energy is available for it, ordinarily at a time complementary to the other prime energy-requiring activities of the annual cycle such as feeding young, migration, and survival of low temperatures (Pitelka, 1958; Kendeigh, 1949: 125). We believe that aerial foraging is a difficult way to make a living compared with many modes of foraging. The appearance of effort when even such skilled fliers as Cedar Waxwings, *Bombycilla cedrorum*, indulge in flycatching suggests this. Further, we believe that attainment of full ability in aerial foraging is an extended process of maturation or practice or both. During most of the approximately 40 days we observed young out of the nest, their flying ability increased. The period of dependence is long in kingbirds. The total period from first egg laid to last observed feeding of fledged young is about 70 days. For an average pair in southern Michigan this means that the young are fed until near the middle of August. We suggest that the energetic demands of caring for the young do not permit molt before this time. Southward migration before cold weather and the decline of flying insects is a necessity (for a graphic account of what may befall kingbirds and other aerial foragers when food supplies and temperatures are low, see Anderson, 1965). Over much of the breeding range of the kingbird, the intervening period would allow only a very rapid molt. For birds so wholly dependent on aerial foraging, a rapid molt might not be energetically feasible if it impaired their flying ability (Johnson, 1963: 882).

We regard many points of this hypothesis as applicable to other flycatchers and aerial foragers in other families. In some cases, the long period of dependency (and maturation) may be spent in the nest (e.g., swallows and *Apus apus*); in others, it may be as in the kingbird, but observations during post-fledging phases of the life cycle are very scant. According to Fry (1967), young of the White-throated Bee-eater, *Merops albicollis*, (which molts on its dry season "wintering grounds" following migration) are dependent for a protracted period of 6–8 weeks after fledging.

(At this point, we are left with a number of aerial foragers that do not molt before migration, including some tyrannids, and also several species that are not aerial foragers but that molt after migration. At the risk of overextending ourselves, we will point out that the latter group reads in part like a list of characteristic nonpasserine species of tundra and northern taiga [see Stresemann and Stresemann, 1966: 36]. For these species, the advantage of postmigratory molt may lie in the necessity for leaving the breeding grounds soon after the young are reared, even though the young do not require extended care. For the rest in both categories, we fall back on the point that has been often made and that is obviously true: Timing of molt is a character that is highly susceptible to selection on the specific level. Species that are able to raise one brood and also molt before migration do so; species that are able to raise two broods and also molt do so; species that are able to raise one brood and also either molt or care for a second brood do one or the other; etc.).

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## SUMMARY

The feeding of young Eastern Kingbirds was studied in Kalamazoo County, Michigan, 1959–66; included were 141 hours of observation during the nestling period and 74 during the fledgling period. Insect imagoes were the main food brought to nestlings and fledglings. Feeding rate increased over the course of nestling life, but the peak rate of feeding came 8–16 days after the young were out of the nest. A long decline followed,

leading to apparent cessation of feeding of young by adults about 35 days after fledging. During the period when the young are leaving the nest, feeding effort is concentrated on the nestlings.

Feeding rate is probably not an accurate reflection of energy supplied to the young; for kingbirds, for day-to-day comparisons, it may serve adequately. A hand-reared fledgling on the sixth day out of the nest consumed about 5 g (dry weight) of insects, or about 27 Kcal.

Fledglings can forage by flycatching 8 days after leaving the nest; however, their flying ability increased over most of the approximately 40 days post-fledging that they were observed.

A hypothesis is put forward to explain the fact that the fall molt of kingbirds occurs after southward migration. It is suggested that the energetic demands of caring for the young over an extended period of time combined with the need to migrate southward before food and weather conditions become unfavorable do not allow an aerial forager a sufficient interval for molting.

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*C. C. Adams Center for Ecological Studies, Department of Biology, Western Michigan University, Kalamazoo, Michigan (Present address of first author, Highland Park Community College, Highland Park, Michigan).*