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GROWTH AND AGING OF NESTLING EASTERN KINGBIRDS AND EASTERN PHOEBES

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Growth rates are integral aspects of avian life histories (Lack 1968) and extensive research has dealt with the relationship of the rate of nestling development to body weight (Ricklefs 1968), rate of nestling mortality (Ricklefs 1969), precocity of development (Ricklefs 1973), diet (Morton 1973, White 1974), and foraging mode (O'Connor 1978). Numerous conclusions have been drawn from the available data, but the accuracy and validity of these conclusions may be suspect considering the nature of past sampling. More extensive sampling is required for birds of diverse foraging strategies and for species nesting at all heights in the vegetation. Second, growth studies often provide methods for aging and/or sexing nestlings (Holcomb and Twiest 1971, Hamel 1974). Accurate estimates of age are useful to researchers investigating the life histories of individual species.

In an extensive review, Ricklefs (1968) gave growth rates for only 2 of the 31 tyrannid flycatchers which breed in North America, perhaps because few species in this family nest at heights amenable to easy study (Harrison 1978). Here I report measurements and descriptions from field observations on the development of 2 tyrannid flycatchers, the Eastern Kingbird (*Tyrannus tyrannus*) and Eastern Phoebe (*Sayornis phoebe*). Measurement data were fit to the logistics curve and estimates of growth parameters were calculated following procedures given by Ricklefs (1967).

STUDY AREA AND METHODS

Data were obtained from free-living flycatchers from mid-April to early August 1980. The main study site was centered near Clinton Lake, 6.5 km west of Lawrence, Douglas Co., Kansas. Other information on phoebes was gathered near the University of Kansas Natural History Reservation, 8 km northeast of Lawrence.

Eastern Kingbird nests were usually found by observing adults carrying nest material or by the aggressive behavior of adults as I approached the nest site. Except for one nest on a small building, all phoebe nests were located under small highway bridges.

Nestlings were marked by clipping a specific toenail. Weight, the tarsus length, and the length of primary 9 (the outermost primary is number 10) of each nestling were measured at about (within 90 min) the same time each day, usually between 1630 and 1930. The length of the tarsus was measured from the tibiotarsus joint to the base of the hind toe. The length of the 9th primary was measured from the point of emergence from the skin to the tip of the sheath or to the tip of the unsheathed feather. Tarsi and primaries were measured with calipers to the nearest .05 mm and nestling weight was estimated to the nearest .1 g with a 50 g Pesola scale. I weighed birds last in the hope that handling would cause the young to defecate and provide weights with less variation.

In addition I noted the general color and markings on the body, the day of appearance of the future primaries as a dark line on the skin of the wings, the emergence of various feather tracts, day of emergence and unsheathing of the 9th primary, and the first opening of the eyes. The day of hatching was designated day 1, since most of the young had completed at least ½ day of growth at the time of initial nest visit. To avoid causing premature fledging, measurements were never made after day 14.

Ricklefs' (1967) method of converting growth curves into straight lines was used to describe the rate of weight increase and tarsal growth. A least squares regression was then calculated to describe the relationship between growth rates and age. This regression coefficient is directly proportional to the overall rate of growth, K. This method requires that asymptotic size be known. Since the 9th primary does not approach an asymptotic size during the nestling period, and because its growth is essentially linear between days 6 and 14, I calculated a least squares regression between percent of adult size and age and used the resulting regression coefficient to estimate rate of growth.

RESULTS AND DISCUSSION

Growth data were obtained for 22 broods of each species (Table 1). For both species, weight on day 1 is a slight overestimate of hatching weight because most young were weighed initially at least several hours after hatching had occurred. For recently hatched young, mean weights were 3.22 g (SD = .420, n = 14) for the Eastern Kingbird and 1.65 g (SD = .158, n = 19) for the Eastern Phoebe. Least squares regression of hatching weight against fresh egg weight in the kingbird accounted for 71% of the variation in hatching weight ($r = .843$, df = 12, $P < .01$) and 59% of the variation in hatching weight in the phoebe ($r = .768$, df = 17, $P < .01$). Hatching weight of both species was approximately 8% of adult weight.

Weight gain was consistently the most variable of the 3 components of growth measured (Table 1). Tarsus length was the least variable. The 9th primary exhibited a pattern of extreme variability during the first few days of growth, due in large part to slight variation in the actual time of emergence from the skin. This variability rapidly decreased as the birds aged. This pattern was true for both species. In comparison to the phoebe, the kingbird was slightly less variable with respect to the length of the tarsus and the 9th primary, but exhibited greater variability in weight gain. In all cases declines in variability with age were significant (least squares regression of CV on age, $P < .01$). This variability at the earliest ages probably diminished due to either death of part of the brood or compensatory growth within the brood. Several factors may

TABLE 1. Mean daily weight, tarsus length, and 9th primary length in the Eastern Kingbird and Eastern Phoebe. Coefficient of variation is given in parentheses.

Age	Eastern Kingbird				Eastern Phoebe			
	N	Weight (g)	Tarsus (mm)	Primary (mm)	N	Weight (g)	Tarsus (mm)	Primary (mm)
Day 1	40	3.58 (17.2)	6.43 (7.7)	—	61	1.91 (19.0)	5.47 (6.8)	—
2	45	5.53 (12.8)	7.52 (7.5)	—	81	2.77 (16.8)	6.25 (6.1)	—
3	52	7.82 (14.1)	8.74 (7.9)	—	79	3.98 (16.4)	7.18 (6.7)	—
4	54	10.36 (13.6)	10.24 (6.9)	.86 (51.6)	80	5.43 (14.9)	8.46 (7.7)	.43 (102.1)
5	53	13.54 (13.0)	11.86 (6.3)	2.60 (25.6)	76	7.10 (14.6)	9.78 (7.5)	1.95 (41.9)
6	52	16.56 (12.9)	13.29 (5.6)	5.19 (18.4)	74	8.89 (12.4)	11.26 (6.8)	4.24 (27.9)
7	49	19.39 (13.8)	14.61 (5.0)	8.49 (14.4)	74	10.96 (10.7)	12.63 (6.0)	7.30 (21.3)
8	47	22.27 (12.7)	15.72 (4.5)	12.43 (11.8)	75	12.51 (9.1)	13.82 (5.1)	10.70 (16.2)
9	45	25.21 (11.8)	16.59 (4.5)	16.34 (9.6)	72	14.22 (8.0)	14.91 (4.7)	14.27 (12.4)
10	43	26.61 (12.0)	17.16 (4.1)	20.43 (8.2)	68	15.36 (9.3)	15.86 (4.1)	18.13 (10.1)
11	42	27.59 (11.4)	17.61 (3.4)	24.36 (7.5)	67	16.32 (8.3)	16.43 (4.3)	21.87 (8.2)
12	40	28.80 (13.3)	17.91 (3.8)	28.15 (6.8)	66	16.91 (9.3)	16.93 (4.3)	25.41 (6.4)
13	38	29.77 (11.5)	18.17 (3.4)	31.89 (5.8)	60	17.16 (10.0)	17.26 (4.2)	28.60 (5.5)
14	21	29.79 (11.0)	18.26 (2.7)	35.13 (4.9)	49	17.47 (8.8)	17.41 (5.0)	31.59 (4.9)

TABLE 2. Age-specific events in the development of the Eastern Kingbird.[a]

Character	Age										
	1	2	3	4	5	6	7	8	9	10	N
Body free of marks	100	—	—	—	—	—	—	—	—	—	29
Dotting of primaries	7	93	—	—	—	—	—	—	—	—	29
Spinal tract darkened	—	7	90	3	—	—	—	—	—	—	27
Humeral tract darkened	—	7	93	—	—	—	—	—	—	—	27
Capital tract darkened	—	3	90	7	—	—	—	—	—	—	27
Wings 40% darkened	—	4	96	—	—	—	—	—	—	—	27
Wings 90% darkened	—	—	4	96	—	—	—	—	—	—	27
9th primary emerges	—	—	14	86	—	—	—	—	—	—	52
Ventral tract, sternal region darkened	—	—	7	93	—	—	—	—	—	—	27
Eyes begin to open	—	—	—	14	54	32	—	—	—	—	35
Emergence of sheaths on the body tracts	—	—	—	—	100	—	—	—	—	—	9
Sheath of 9th primary breaks	—	—	—	—	—	—	—	18	65	17	54

[a] Values are given as the percentage of the total number of observations.

contribute to the high variability in weight gain, including differences in hatching size, order of hatching, brood size, time of season, variability of weather conditions, differences in productivity among sites, or sexual size dimorphism.

Aging of nestlings.—Young should be aged using a combination of several characters. Not only do characters differ in their ability to accurately predict age, but the accuracy of the estimates from any particular character usually changes with age. Weight is the most common single indicator of age used in many studies, but weight is actually less reliable than many other characters. The most reliable characters are those which are currently changing fastest. The use of measurement variables should be supplemented with easily observed qualitative changes in appearance, such as the time of emergence of particular feather tracts or unsheathing of particular feathers. These events are often very age specific (Tables 2 and 3).

The procedure I recommend for aging phoebe and kingbird nestlings is based upon characteristics of the 9th primary. First, if the 9th primary has not yet emerged from the skin (Tables 2 and 3), then separate estimates of age are obtained from comparisons to weight and tarsus data (Table 1). Their average is the estimated age. If the 9th primary has already emerged, but its feather sheath has not split, then age is best estimated as the average of the ages separately obtained from comparisons to weight, and tarsal and 9th primary lengths (Table 1). The best estimate of age after the sheath of primary 9 has split is obtained by averaging the ages estimated from measurements of tarsal and 9th primary lengths (Table 1). These estimated ages can then be compared to the age-specific occurrence of the events outlined in Tables 2 and 3.

TABLE 3. Age-specific events in the development of the Eastern Phoebe.[a]

Character	Age 1	2	3	4	5	6	7	8	9	10	11	N
Body free of marks	100	—	—	—	—	—	—	—	—	—	—	45
Dotting of primaries	—	89	11	—	—	—	—	—	—	—	—	45
Spinal tract darkened	—	—	22	78	—	—	—	—	—	—	—	40
Humeral tract darkened	—	—	25	75	—	—	—	—	—	—	—	40
Wings 40% darkened	—	—	38	62	—	—	—	—	—	—	—	8
Wings 90% darkened	—	—	—	44	56	—	—	—	—	—	—	18
Capital tract darkened	—	—	3	52	45	—	—	—	—	—	—	33
9th primary emerges	—	—	—	81	19	—	—	—	—	—	—	43
Ventral tract, sternal region darkened	—	—	12	38	50	—	—	—	—	—	—	42
Eyes begin to open	—	—	—	—	—	46	30	24	—	—	—	37
Sheath of 9th primary breaks	—	—	—	—	—	—	—	2	45	45	8	65

[a] Values are given as the percentage of the total number of observations.

Changes in major components and plumage development.—Increases in weight and in the length of the tarsus followed the logistic curve typical of passerine birds (Ricklefs 1968). The growth of the 9th primary was almost linear over the period of measurement, although it is best described by a logistic curve. Logistic inflection points are given in Table 4. Strictly speaking, the inflection point is the location where 50% of asymptotic size is reached (Ricklefs 1967). It also represents the period of time over which growth is maximum, and presumably energy demands the highest. Since the asymptotic size of the 9th primary was not known, the inflection point was estimated to occur at the age where the absolute increase in length was greatest. In both species growth rate peaked earliest in the tarsi, at day 3 or 4 in the kingbird and one day later in the phoebe. The tarsi continued to gradually increase in length at a decreasing rate up to day 14. Initially weight gain was relatively slow, then increased and was maintained at a high rate up to day 9 in the kingbird and day 10 in the phoebe. The kingbird exhibited a more marked decrease in daily weight increments than the phoebe after this time. The inflection point for weight gain in the kingbird occurred between days 5 and 6, slightly earlier than in the phoebe. In both species the 9th primary first emerged from the skin on day 4 (Tables 2 and 3). Maximum growth occurred between days 9 and 10 (Table 4), at a time when weight gain began to level off. In both species the inflection point of the three curves do not overlap (Table 4).

The young of both species hatched with a relatively heavy covering of down. In general, plumage development was slow until days 5 or 6. The most conspicuous changes prior to this were in overall body size. The primaries first appeared as thin lines on the skin of the wings, followed by a more rapid development of the body feather tracts (Tables

TABLE 4. The age of occurrence of the inflection point in the growth curves for weight, the tarsus, and the 9th primary for the Eastern Kingbird and Eastern Phoebe.

Component	Average age (days)	
	Kingbird	Phoebe
Tarsus[a]	3.5	4.5
Weight[a]	5.5	6.1
9th primary[b]	9.5	10.0

[a] Inflection point = the point on the plot of converted weights (C_w) (Ricklefs 1967) against age where $C_w = 0$.
[b] Inflection point is estimated to occur where the daily change in size is greatest.

2 and 3). Feather tracts of the dorsal surface developed slightly ahead of those of the ventral surface. The importance of covering the exposed, dorsal surface from the elements is the probable cause for this pattern. It would reduce heat loss and allow adults to spend less time brooding and more time foraging. The pin feathers of most body tracts did not emerge from the skin until days 5 or 6, slightly later than the age of emergence of the 9th primary from the skin. Contour feathers emerged from sheaths about 2 days before the remiges did. Body plumage developed rapidly after day 6. Contour feathers apparently matured during the period of greatest weight gain and at a more rapid rate than did flight feathers. By days 9 and 10 contour feathers were sufficiently dense to cover a crouched bird in the nest. At this age the remiges broke their sheaths and began to mature. Nestlings of both species took on an adult appearance by days 13 and 14.

The general pattern of growth is characterized as a process of staggered development and resource allocation to the component (weight, locomotory organ, insulative cover) with the highest functional priority (Table 4; O'Connor 1977) at a given time. Staggered peaks in energy demand should tend to reduce the overall maximum amount of energy required by each nestling and the brood on any particular day. The order is such that they fulfill current needs. Thus, young hatch with legs and feet relatively mature and are able to orient towards adults and maintain position in the nest. The peak in growth of the feet is also early. The period of maturation of the flight feathers is delayed and does not occur until after the body plumage is nearing the end of development. Development of this insulative cover, particularly the dorsal plumage, as well as maintenance of a more favorable surface area-to-volume ratio as the birds age and gain weight, are requirements for thermoregulation (Morton and Carey 1971, O'Connor 1977). In general, initiation of thermoregulation coincides with a leveling in weight gain and rapid maturation of remiges (Yarbrough 1970, O'Connor 1975). Mahan (1964) found that Eastern Phoebes first began to effectively thermoregulate by day 10, as would be predicted from the pat-

TABLE 5. Rate of growth and relative size attained in body weight, tarsus length, and 9th primary length.

	Weight[a]		Tarsus[a]		9th primary[b]	
	Kingbird	Phoebe	Kingbird	Phoebe	Kingbird	Phoebe
Asymptotic size	30.2	18.1	19.0	18.2	36.6	32.0
Adult size	39.1	19.7	19.4	18.3	87.3	63.8
Relative size	.77	.92	.99	.99	.42	.50
Growth rate, K	.436	.431	.332	.320	4.38	5.50
Growth rate, t_{10-90}	10.1	10.2	13.2	13.7	—	—
Growth index, G	1.49	1.36	1.44	1.24	—	—
Proportionate 9th primary length	—	—	—	—	25.5	23.6

[a] Asymptotic size, growth rate, and growth index (at 13 days of age) calculated using methods of Ricklefs (1967).
[b] Day 14 length used in place of asymptotic size. See text for full explanation.
[c] Proportionate length = (length of the adult 9th primary)/(adult weight)$^{1/3}$ (Amadon 1943).

terns reported here. O'Connor's (1977) view that the development of altricial nestlings is "adaptively organized" is also supported by these data.

Growth rates.—The rates of increase in body weight were nearly identical in both phoebes and kingbirds, despite large differences in adult weight. The tarsi also grew at nearly the same rate, though slower than body weight (Table 5). The points of inflection for the tarsi occurred earlier than either weight or primary length (Table 4), probably because the tarsi were near 30% of adult size at hatching. Young weighed less than 10% of adult weight at hatching. Therefore, the larger relative size of the tarsi at hatching allowed them to reach 50% of adult size sooner, despite the faster rate of growth for weight gain. Tarsi are adult-size when young fledge, but fledging weight is below adult weight (Table 5). Ricklefs (1968) reported similar growth rates for the Willow Flycatcher (*Empidonax trailii*) (K = .472) and the Western Flycatcher (*E. difficilis*) (K = .436). The rate of weight gain in birds with altricial young has been reported to be inversely correlated with body weight (Ricklefs 1968), but no such pattern is found in these four species.

Growth of the 9th primary was more rapid in the Eastern Phoebe. By day 14, 3 to 4 days before leaving the nest, primaries had reached 50% of adult length. Primaries of 14-day-old kingbirds were only 42% of adult size, even though they leave the nest at the same age as phoebes. The apparent differences may be related to the relatively shorter wings of adult Eastern Phoebes (Table 5).

SUMMARY

Growth and development of nestling Eastern Kingbirds and Eastern Phoebes were studied in Kansas in 1980. Daily changes in weight and tarsus and 9th primary length are presented with descriptions of age specific developmental traits. A procedure is outlined to age nestlings found after hatching. Growth of both species, in terms of rates of change and sequence of developmental changes, are very similar and support the hypothesis that the altricial mode of development is adaptively organized to allow the majority of food delivered to the young to be used for growth. The rates of growth for weight in these species are similar to published rates of other flycatchers.

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LITERATURE CITED

AMADON, D. 1943. Bird weights as an aid in taxonomy. Wilson Bull. 55:164–177.

HAMEL, P. B. 1974. Age and sex determination of nestling Common Grackles. Bird-Banding 45:16–23.

HARRISON, C. 1978. A field guide to the nests, eggs and nestlings of North American birds. Collins Sons and Co., Glasgow.

HOLCOMB, L. C., AND G. TWIEST. 1971. Growth and calculation of age for Red-winged Blackbird nestlings. Bird-Banding 42:1–17.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MAHAN, H. D. 1964. The effect of the environment on growth, development and temperature regulation in nestling Eastern Phoebes. Ph.D. dissertation, Michigan State University, East Lansing, Michigan.

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

MORTON, M. L., AND C. CAREY. 1971. Growth and development of endothermy in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*). Physiol. Zool. 44:177–189.

O'CONNOR, R. J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling Blue Tits *Parus caeruleus* and House Sparrows *Passer domesticus*. J. Zool., Lond. 175:391–403.

———. 1977. Differential growth and body composition in altricial passerines. Ibis 119:147–166.

———. 1978. Growth strategies in nestling passerines. Living Bird 16:209–238.

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–983.

———. 1968. Patterns of growth in birds. Ibis 110:419–451.

———. 1969. Preliminary models for growth rates of altricial birds. Ecology 50:1031–1039.

———. 1973. Patterns of growth in birds: growth rate and mode of development. Ibis 115:177–201.

WHITE, S. C. 1974. Ecological aspects of growth and nutrition in tropical fruit-eating birds. Ph.D. dissertation, Univ. of Pennsylvania, Philadelphia.

YARBROUGH, C. G. 1970. The development of endothermy in nestling Gray-crowned Rosy Finches, *Leucosticte tephrocotis griseonucha*. Comp. Biochem. Physiol. 34:917–925.

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