GROWTH AND DEVELOPMENT OF EASTERN BLUEBIRDS

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INTRODUCTION

Descriptive data on avian growth rates have been used for aging (Hamel, 1974) and sexing (Holcomb and Twiest, 1970), for analyzing differential wing and leg growth (Olendorff, 1973), for examining the effects of variations in clutch size (Lack and Silva, 1949; Ricklefs, 1968; Holcomb, 1970) and hatching order (LeCroy and LeCroy, 1974), and for retrospective dating of events in the breeding season, especially hatching (Williams, 1959). Conclusions can be drawn on such matters once the normal growth rate is established for any given species. The reliability of these conclusions for individual birds is dependent upon the normal variation in development and may vary interspecifically and for different growth parameters (Ricklefs, 1968).

Little information is available on development in the Eastern Bluebird (*Sialia sialis*). Hamilton (1943) weighed three broods of *S. sialis*, and Donahoe (1939) and Smith (1937) gave general accounts of bluebird nestling development. This paper describes development for Eastern Bluebirds in southern Michigan. Parameters chosen were: (1) body and plumage measurements for young of various ages, (2) overall changes in the physical appearance, (3) ages of young that leave the nest undisturbed, (4) ontogeny of behavior, and (5) body weight changes. Characteristics of normal development in this species are then used to assess the effects of season and brood size on growth rate, and to make comparisons with other New World thrushes.

METHODS

"Free-living" Eastern Bluebirds were examined in Macomb County, Michigan from 1970 to 1975. Bluebirds nested there in nesting boxes similar to those used by Laskey (1940). Two areas of investigation, postfledging development and diurnal weight variation of nestlings, were explored using captive birds reared by "wild" (= not tame) adult bluebirds that bred in large aviaries (Pinkowski, 1975a), were offered unlimited food (insects and fruit) and water, and were subjected to natural photoperiods. Observations on postfledging development and frequent weighing of free-living birds were nearly impossible or unduly disturbing, and the results obtained on the captive birds are considered typical because development in these birds was normal in other respects (fledging age, weight increases, age for attainment of independence, all approximating the corresponding data obtained for free-living birds).

Individual nestlings were marked with a felt-tipped marker on the tarsi immediately after hatching and were banded at the end of the first week for identification. All birds were weighed and measured at the same time each day, usually at 1800-2000, whenever possible. All measurements were plotted and interpolated for each bird to calculate the values for young of various ages. Body and plumage measurements were interpolated on a 24-hour scale. Weights, however, were interpolated in terms of daily feeding periods. Using this procedure, a bird hatched at dawn is 1 day old at dusk on the same day, 2 days old at dusk the following day, etc. (only diurnal periods when the adults were feeding were included on the time scale for interpolation purposes). Although it might be argued that such a procedure ignores overnight weight loss, I found that the morning weights of birds were invariably within 95% of the weight at the completion of feeding on the previous night. This slight weight loss is regained quickly when the adults commence feeding upon awakening.

Only weights and measurements for young that did not die of starvation or exposure were included in the mensural tabulations. Measurements taken included the following: (1) body length, measured with the neck withdrawn; (2) body weight, determined to the nearest 0.1 g with a triple-beam balance; (3) wing chord, the distance from the bend of the wrist to the tip of the manus or to the tip of the longest primary, depending on the age of the bird; (4) tail length, the distance from the center of the tail base to the tip of the longest rectrix; (5) outer primary web, the extent which the outermost full-length primary (primary number 9, since number 10 is spurious) was free of the sheath; (6) central tail feather web, the sheath-free portion of the central rectrix (often the values of the right and left feathers were averaged for the central tail feather web and the outer primary web); and (7) tarsus length, measured from the posterior of the tibiotarsal joint to the posterior of the hind toe base. Sample sizes differed for different parameters and age groups because occasionally a brood was lost to a predator during development and some broods were measured only in the later stages of development.

I made daily observations of nests in the study area with a high power spotting scope to determine the age at nest departure for nestlings. This procedure was necessary because almost any disturbance after the second week of the nestling period will cause bluebird nestlings to fledge prematurely (Hartshorne, 1962; White and Woolfenden, 1973; Pinkowski, 1974a).

All linear measurements are in millimeters and weights are in grams. The day of hatching is designated as day 0, the day after hatching as day 1, etc.

RESULTS AND DISCUSSION

Body and Plumage Measurements

Nestlings.—Measurements for young birds of various ages are summarized in Table 1. The mean coefficients of variation for each character, calculated by considering only those values listed that are greater than zero, are as follows: body length, 0.0436 $<$ wing chord, 0.0626 $<$ tail length, 0.1313 $<$ outer primary web, 0.4838 $<$ central tail feather web, 0.5293. As expected, relative variability for characters dependent upon feather unsheathing (outer primary web and central tail feather web) is significantly

TABLE 1.

Body, wing, and tail growth in nestling Eastern Bluebirds.

Age in days	Body length	Wing chord	Outer primary	Center tail feather	Tail length
0	35.15 ± 1.76 (10)[1]	6.85 ± 0.24 (10)			
1	39.22 ± 1.05 (16)	7.54 ± 0.48 (13)			
2	43.43 ± 1.42 (22)	8.55 ± 0.57 (16)			
3	48.15 ± 1.67 (15)	9.59 ± 0.44 (11)			
4	52.30 ± 3.21 (20)	12.38 ± 0.83 (16)			
5	56.57 ± 3.30 (18)	14.98 ± 1.21 (16)			
6	60.68 ± 1.57 (14)	17.70 ± 1.58 (11)			
7	64.99 ± 2.88 (14)	21.88 ± 2.21 (10)			
8	68.91 ± 2.93 (16)	27.15 ± 2.34 (13)	0.00 ± 0.00 (14)	0.00 ± 0.00 (10)	
9	73.02 ± 2.90 (21)	32.93 ± 2.08 (21)	0.21 ± 0.38 (10)	0.14 ± 0.22 (12)	
10	77.24 ± 3.02 (18)	40.03 ± 2.76 (23)	0.97 ± 0.85 (23)	0.77 ± 0.60 (24)	9.48 ± 1.60 (12)
11	83.43 ± 5.45 (11)	45.92 ± 2.71 (23)	3.38 ± 1.53 (32)	1.94 ± 0.82 (23)	14.05 ± 1.56 (12)
12	86.03 ± 3.90 (16)	50.00 ± 2.82 (28)	6.78 ± 2.10 (40)	3.25 ± 1.23 (28)	16.91 ± 1.93 (13)
13	89.92 ± 4.45 (18)	54.43 ± 2.95 (33)	11.18 ± 2.80 (42)	4.75 ± 1.64 (33)	20.08 ± 1.77 (12)
14	96.19 ± 4.25 (14)	58.70 ± 2.84 (33)	16.09 ± 3.40 (42)	6.79 ± 2.29 (34)	21.61 ± 3.01 (15)
15	99.18 ± 5.69 (17)	61.86 ± 2.98 (27)	19.67 ± 3.50 (37)	8.71 ± 2.82 (28)	24.32 ± 4.51 (12)
16	105.78 ± 4.23 (17)	64.83 ± 2.70 (24)	23.44 ± 3.51 (30)	11.03 ± 3.61 (26)	27.01 ± 4.55 (11)
17	111.43 ± 3.09 (3)	67.13 ± 3.50 (16)	26.33 ± 3.06 (18)	12.94 ± 3.60 (17)	31.06 ± 2.33 (5)

[1] All values in mm, written in the form: mean ± SD (n).

greater than that of each of the other characters (*F*-test, $P < 0.01$ using squares of the mean coefficients of variation; Lewontin, 1966).

Although these data describe the developmental rate for a typical nestling, much variation may occur from one nest to another or within a single nest even if all young hatch on the same day, as is usually the case. Table 2 compares young of the same age from three different nests measured during the study. Some of the nestlings were as much as two or three days ahead of others in development. This variation is normal, and even within the individual nests one nestling is nearly two days more advanced than others. Such variation precludes the possibility of accurately aging the young by plumage measurements alone, as Hamel (1974) did with the Common Grackle (*Quiscalus quiscula*).

TABLE 2.
Variation in plumage development of 14-day-old nestlings in different nests.[1]

Number of young	Wing chord	Outer primary web	Center tail feather web
3	51.5 (49.4-54.5)	9.1 (8.7-9.7)	3.3 (2.6-4.0)
4	53.9 (51.7-56.0)	9.6 (8.1-11.6)	3.6 (3.2-4.6)
4	57.9 (54.8-60.8)	12.6 (10.7-14.3)	4.9 (4.2-5.2)

[1] Values are in mm in the form: mean (range).

Fledglings.—Wing development in fledglings is summarized in Figure 1. Rate of increase in wing length is greatest shortly before fledging (day 14; see Table 1), but the wing continues to increase slowly in length after fledging. A similar pattern was also observed in the cavity-nesting Cactus Wren (*Campylorhynchus brunneicapillus*) and European Starling (*Sturnus vulgaris*) by Ricklefs (1975, pers. comm.).

Adult Eastern Bluebirds measured in the study area showed an average wing chord of 99.2 mm (SD = 3.7, n = 25). The wing is slightly longer in males ($\bar{x}$ = 101.1 mm, SD = 3.3, n = 15) than in females ($\bar{x}$ = 96.4 mm, SD = 2.2, n = 10). Fledglings attain the adult dimensions for wing chord at the age of 35-40 days, which corresponds to the period when juveniles cease to be fed by the parents and become independent (see below). Examination of the values in Figure 1 for the outer primary web indicates that some unsheathing of the remiges (and other feathers as well) may occur after an age of 40 days, and the adult primary web length ($\bar{x}$ = 72.5 mm, SD = 2.9, n = 15) may be attained several days later in some individuals.

General Description of Nestling Development

Physical attributes characterizing young bluebirds of different ages that develop at a normal rate are summarized below.

The Hatchling.—Weights of wet bluebird hatchlings not yet fed

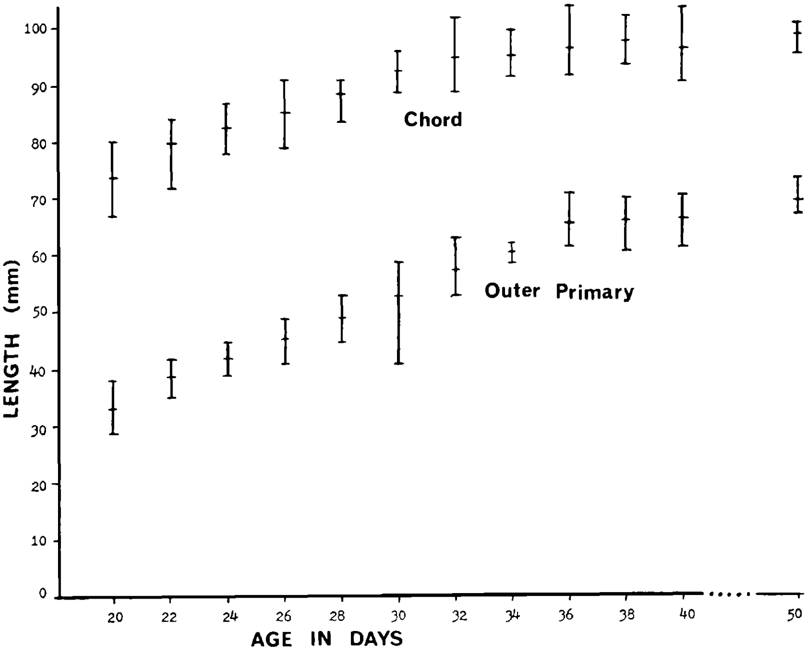

FIGURE 1. Range and mean values for wing chord and outer primary web lengths in fledgling Eastern Bluebirds, based on birds reared by adult bluebirds in captivity. Sample sizes for each of the successive age classes were, respectively: 10, 14, 7, 9, 12, 4, 5, 4, 7, and 7.

by adults ranged from 1.7-3.1 g ($\bar{x}$ = 2.4 g, SD = 0.48, n = 16) and averaged 8.0% of the mean adult weight (given below). Hatchling weight was found to depend on the size and shape of the egg. Young hatched from unusually small eggs ($\bar{x}$ = 19.0 × 15.3 mm, n = 5) had an average weight of 1.8 g. The mean weight of hatchlings from normal sized eggs ($\bar{x}$ = 20.8 × 16.4 mm, n = 5) was 2.4 g, and young from eggs larger than normal ($\bar{x}$ = 22.4 × 17.7 mm, n = 6) had an average weight of 2.8 g. Egg diameter correlated more closely with hatchling weight (r = 0.980, $P < 0.001$) than did egg length (r = 0.871, $P < 0.001$), i.e., the two correlation coefficients are significantly different ($P < 0.05$), partly because egg volume is directly proportional to the first power of egg length and to the second power of egg diameter (Preston, 1974).

Parsons (1970) found that young Herring Gulls (*Larus argentatus*) hatched from larger eggs had greater survival than young hatched from smaller eggs; Schifferli (1973) noted a positive correlation between egg weight in the Great Tit (*Parus major*) and developmental rate during the first 8 days of the nestling period. These relationships may exist in *S. sialis*, but the situation is complex. For example, egg size gradually increases with laying order (Pinkowski, 1974b), which suggests that young hatched from the last eggs laid are larger at hatching and may develop more rapidly or have greater survival than their siblings. The eggs, however, usually hatch in the approximate order of laying, and the earliest young to hatch may gain a slight size advantage over those that hatch later.

The bluebird hatchling is completely psilopaedic except for scattered, dingy-gray down feathers or pre-pennae. These occur on the capital tract, in the scapular region of the humeral tract, and along the dorsal midline (spinal tract). The humeral pre-pennae are in a single row; those of the spinal region occur in two rows. The future remiges and rectrices are barely noticeable, appearing as tiny spots that may have thin filaments (discussed by Boulton, 1927) protruding from the surface. The tarsi average 6.3 mm (SD = 0.76) in length.

First Week.—A 1-day-old bird is similar to the hatchling except for its larger size. Down feathers are more conspicuous on day 1 due to an increase in their length (to 6-14 mm) during the first 24 hours. On day 2 contour feather development is underway in several regions, including the spinal, humeral, and ventral tracts, where rows of tiny spots can be seen.

On day 3 the feathers of the femoral tract are emerging; the entire tract measures 7-8 mm in length. In the caudal and alar tracts short, light-colored feather shafts now barely project beyond the skin. By day 4 the wings are generally dark throughout, and the future rectrices project 1-2 mm caudad. Feather growth is slow at this time, although body size is increasing very rapidly. Even the tarsi are growing at their most rapid rate, which is critical because of the importance of the legs and feet in balance and reach of the hungry young.

Day 5 marks the appearance of feathers in the crural region (a few scattered dark spots) and a continued darkening of the capital and humeral tracts. From the elbow outward the dorsal surface of the wing is now completely dark and the shafts of the future coverts are beginning to emerge. On day 5 or 6 the eyes begin to open. Feathers emerge from sheaths in the posterior ventral, femoral, and scapular tracts, and long (0.5-2 mm) sheathed feathers are prominent in the spinal, crural, and capital tracts.

Second Week.—During the first week the greatest change in nestlings is an overall increase in body size (Table 1); the second week is a period of rapid feather growth and unsheathing. Feathers of the ventral tract (especially the white feathers posterior to the knee) are well out of the sheath by day 7, some 3-4 mm long. The dorsal surface of the capital region is now covered with feathers in sheaths; the chin and throat are sparsely covered. Feathers of the anterior surface of the humeral tract are emerging from the sheaths.

On day 8 the secondary wing coverts, especially the greater coverts, break out of the sheaths. The primaries and secondaries are growing rapidly, although remaining in sheaths. On day 9 feathers are out of the sheaths in the capital (especially near the center), alar (secondaries), and caudal (rectrices) tracts. At this age the caudal feathers barely project beyond the vent.

On day 10 or 11 most of the feathers of the capital tract, all secondaries, and at least the innermost primaries, have emerged. Bare, unfeathered areas still exist along the mid-ventral line and between the spinal and femoral tracts. The last feathers of the capital tract are emerging, especially in the frontal, ear, and eye regions; the ear opening is hidden. The tarsi are now about 20 mm long. The nestling is active and exhibits fear if handled and will actively crawl away, a behavior also seen in some 9-day-old nestlings.

By day 12 the nestling is completely feathered except for the mid-ventral region. Feathers near the beak may still be in sheaths. On day 13 the anterior half of the ventral surface is feathered, leaving only a small bare area of skin around the underside of the vent and tail.

Third Week.—Motor coordination develops during the third week. For example, the nestlings become increasingly nervous when handled. Donahoe (1939) noted that young bluebirds at the beginning of their third week orient toward the nest site opening for the first time.

A 14-day-old bird appears sleeker than one of 13 days. Unfeathered areas can no longer be seen under the wings and around the vent (except ventrally). The tarsi now measure 21-22 mm. By day 15 the young bird is completely feathered.

Age of Nest Departure

The mean fledging age for undisturbed young was 18.8 days (SD = 1.47 days, n = 184). No birds left the nest at 15 days or earlier. There were 13 departures at 16 days, 10 at 17 days, 40 at 18 days, 66 at 19 days, 21 at 20 days, 16 at 21 days, and 18 at 22 days.

All instances of nest departures after 20 days occurred in spring nests, and the mean nestling period was longer for spring nests ($\bar{x} = 19.39$ days) than for summer nests ($\bar{x} = 18.63$ days). This difference is significant by the two-tailed t-test ($t = 3.08$, df = 158, $P < 0.01$), and seems to reflect the colder conditions and the accompanying reduction in food resources that exist in spring at northern latitudes. A 25-day nestling record for Michigan (Kenaga, 1961) appears exceptional, especially since it occurred in a summer nest. The longest interval from the onset of incubation until fledging (43 days, which included an unusual 21-day incubation period; Pinkowski, 1974c) occurred in a spring nest, and the shortest (30 days) was noted for a summer nest.

Ontogeny of Behavior

The occurrence of various behavior patterns in nestlings and fledglings is summarized in Table 3. The data are based on my observations of 116 juveniles, including 42 captive birds observed daily from hatching to independence. A special nest box constructed with one of the wooden sides replaced by a screen permitted observation of captive nestlings.

Table 3.

Occurrence of various behavior patterns in young Eastern Bluebirds.[1]

Behavior	Age in days																					
	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48
Huddle together	C	C	C	C	C	C	C	C	C	C	C	C	C	+	+	—	—	—	—	—		
Gape toward adults		—	—	+	+	C	C	C	C	C	C	C	C	C	C	C	C	C	+	+	—	
Preen		—	+	+	+	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Stretch			—	+	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
Exercise wings			—	+	C	C	C	+	—													
Stand on rim of nest					—	+	C	—	—													
Look out nest cavity					—	—	C	—	—													
Poke at grasses					—	+	C	C	C	C	C	C	C	C	+	+	+	+	+	+	+	+
Sunning								+	+	C	C	C	C	C	C	C	C	C	C	C	C	C
"Freezing"								C	C	C	+	+	+	—	—	—	—	—	—	—		
Land on top of each other								C	C	+	—	—	—	—								
Drink water								—	—	+	+	+	C	C	C	C	C	C	C	C	C	C
Bathe									—	—	+	+	C	C	C	C	C	C	C	C	C	C
Fly to adult for food									—	+	C	C	C	C	C	+	+	—	—	—	—	
Bill-wiping										—	+	C	C	C	C	C	C	C	C	C	C	C
Eat small items										—	+	+	C	C	C	C	C	C	C	C	C	C
Alarm chatter										—	—	—	+	+	C	C	C	C	C	C	C	C
Aggressive behavior											—	—	+	+	+	+	+	+	C	C	C	C
Eat large items											—	+	+	+	+	C	C	C	C	C	C	C
Look in cavities													—	—	—	+	+	+	C	C	C	C
Enter cavities																—	+	+	+	+	C	C

[1] Each behavior pattern is listed as common (C), occasional (+), uncommon (—), or absent (not marked) relative to its normal frequency and not relative to other behaviors.

Development of self-feeding in the Eastern Bluebird is similar to that of the Mountain Bluebird (*S. currucoides*) as reported by Pinkowski (1975a) except that true "hovering" (searching for prey while airborne) does not appear as a feeding method in the Eastern Bluebird. Initial self-feedings occur at 22-28 days ($\bar{x}$ = 25.4 days for 28 birds observed regularly) and consist of gleaning small items from a perch or obtaining small insects on the ground by "hopping." Later (28-34 days), prey is located from a perch and seized after a short flight to the ground ("dropping") in the usual manner of adult Eastern Bluebirds. "Flycatching" (the capture of aerial insects) and "fluttering" (remaining airborne before seizing previously located prey) occur at 34-40 days. The parents normally continue to feed the young until they are about 35-40 days old, although a male once fed a 47-day-old juvenile.

Several writers (Wetherbee, 1933; Nice, 1943; Hartshorne, 1962; Pinkowski, 1975b) have commented on the tendency of fledgling bluebirds to feed other young conspecifics. These feedings may involve fledglings feeding other fledglings, or food may be taken to a nest and excreta removed. I found cases of "juvenile helpers" uncommon in the wild, partly because some adults (especially females) do not tolerate fledglings around nest sites. When juveniles do feed other young, food items are "handed over" and not placed far down in the throat. Preparation is poor, and many items are delivered alive and wriggling. This behavior was observed in one young only 37 days old and thus may begin about the time some juveniles reach independence. Several juveniles fed after the onset of their postjuvenal molts.

Nestling Weights

Normal Weight Increases.—Both weight and rate of weight gain of nestlings increase through the fifth day (Fig. 2). Weight then continues to increase but rate decreases, i.e., the inflection point in the curve occurs when the young reach a mean weight of 14.1 g at the end of day 5. At day 12 the nestling weight curve levels off and approaches an asymptote of 27.2 g or 90.7% of the adult weight ($\bar{x}$ = 30.0 g, SD = 1.38, n = 16 birds weighed in the study area, including 10 males and 6 females). Maximum weights of individual birds occurred on day 10 (2 cases), 11 (3), 12 (3), 13 (4), 14 (4), 15 (3), 16 (3), 17 (3), and 18 (1); $\bar{x}$ = 13.81 days. Maximum weight for all nestlings (31.8 g) was recorded for a 14-day-old female.

Growth curves of most passerines follow the logistic pattern characterized by an inflection point that occurs when 50% of the weight asymptote is attained (Ricklefs, 1968). Growth rates for species that follow such a pattern can be compared by employing several useful parameters.

One measure of growth rate, $t_{10\text{-}90}$, the time required for growth of 10% to 90% of the asymptotic weight, is 9.0 days for the bluebird (Figs. 2, 3). For nestling American Robins (*Turdus migratorius*) in the same study area, $t_{10\text{-}90}$ = 7.5 days (Fig. 3), less than the bluebird figure but near an average value of 7.9 obtained

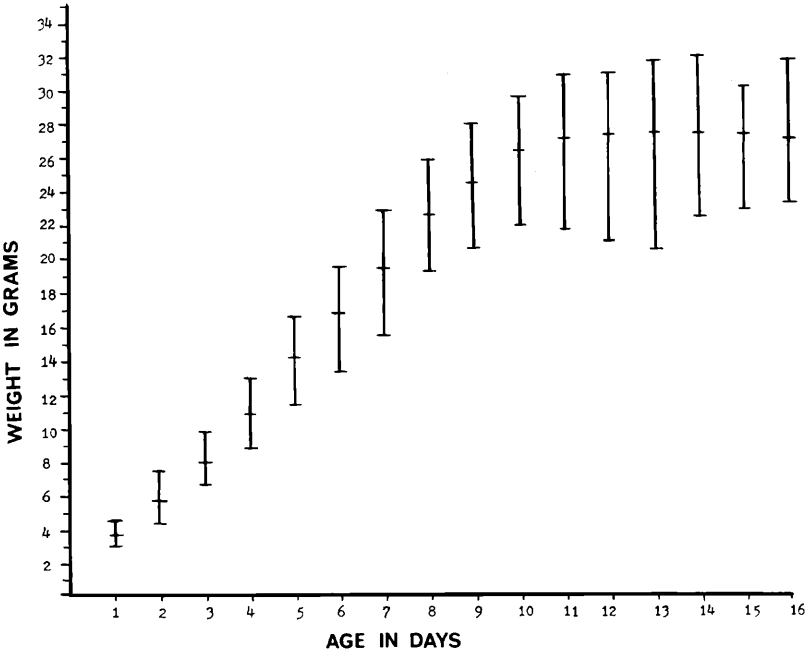

FIGURE 2. Weights of nestling Eastern Bluebirds. For each age class the maximum, mean, and minimum are shown. Sample size for days 1-14 was 35-45 individuals; for day 15 n = 31 and for day 16 n = 17.

for the Hermit Thrush (*Catharus guttata*) in Michigan by Perry and Perry (1918) and Stanwood (1910) (both in Ricklefs, 1968; originals not seen). The importance of these results appears related to nest site location (discussed below).

Weight curves can be transformed into straight lines by calculating a converted weight, C_w, for each mean weight (Ricklefs, 1967). For a logistic curve, $C_w = 1/4 \log_e (W/1\text{-}W)$ for a weight W expressed as a decimal fraction of the weight asymptote. Converted Eastern Bluebird weights are shown in Figure 4. The inflection point on the weight curve (t_{50}) corresponds to the point where $C_w = 0$ on the plot of the converted weights. The slope of the line formed from the converted weights, dW/dt, is 0.122 and the overall growth rate constant, *K*, is 4dW/dt for species that follow the logistic pattern or 0.488 for *S. sialis.*

Using the logistic equations derived by Ricklefs (1967) and the data in Figures 3 and 4, the weight of bluebird nestlings can be calculated as a function of the age in days, t, from t_{10} to t_{90} as follows:

$$\text{Weight (g)} = \frac{\text{Weight Asymptote}}{1 + e^{-K(t - t_{50})}} = \frac{27.2}{1 + e^{-0.488(t - 5.0)}}.$$

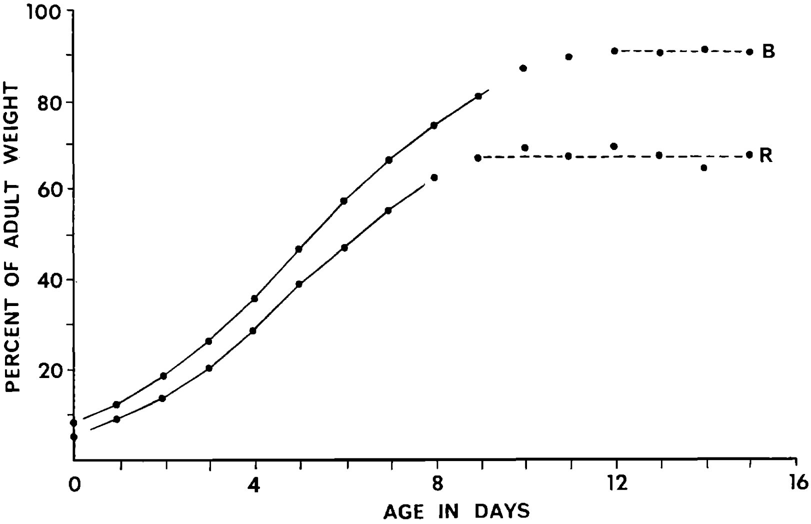

FIGURE 3. Weight curves for nestling Eastern Bluebirds (B) and American Robins (R) given as percentages of the adult weights. The periods when the weight curves are asymptotic are in dashes; the solid lines represent the time when nestlings acquire from 10 to 90% of the asymptotic weight (t_{10}-$_{90}$). The robin data are based on 13 young in 5 nests, with the value for adult weight ($\bar{x}$ = 82.7 g, SD = 7.64) sampled from 6 males, 6 females, and 3 birds of unknown sex. Bluebird adult values are given in the text; nestling weight samples are as in Figure 2.

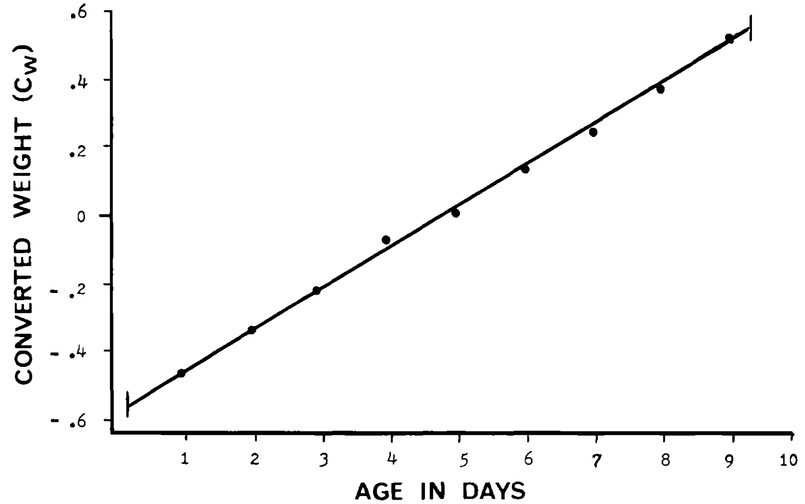

FIGURE 4. Converted weights (C_W) of *S. sialis* nestlings during the growth period t_{10}-$_{90}$. Weights used are those expressed as a percentage of the weight asymptote (Fig. 3).

Comparisons.—*S. sialis* is a cavity nesting species with a relatively long nestling period (16-22 days) and we would expect a reduced growth rate in that species compared to *T. migratorius*, an open-nester with a shorter nestling period (12-15 days; pers. obs.). However, I found little evidence for this. Using the robin weights shown in Figure 3, $K = 0.425$; this is less than the 0.488 value obtained for *S. sialis*. This unexpected result could be based on an underestimation of the asymptotic weight of robin nestlings; it may also be attributable to sampling error because fewer robins were weighed. Other studies, however, indicate only a slightly more rapid growth rate in the robin (with K values given as 0.492 and 0. 504 by Ricklefs, 1968) than in the bluebird. The difference in the lengths of the nestling periods of the two species appears more related to factors other than growth rate such as the difference in nestling size relative to the adult at fledging. The ratio of the asymptote to the adult weight, *R*, is much less for the robin (55.9; 82.7, or 0.676) than for the bluebird (0.907).

Wing growth proceeds more rapidly in the robin (Fig. 5), permitting an earlier nest departure by young robins. Wing chord is greater in the bluebird at fledging (70-75% of the adult value) than it is for the robin at fledging (60-65%). Balph (1975) found that average wing chord in the open-nesting Brewer's Blackbird (*Euphagus cyanocephalus*) at the time of nest departure (13 days) was 63% of the adult value. This result is similar to my figure for *T. migratorius* but less than the value obtained for *S. sialis*.

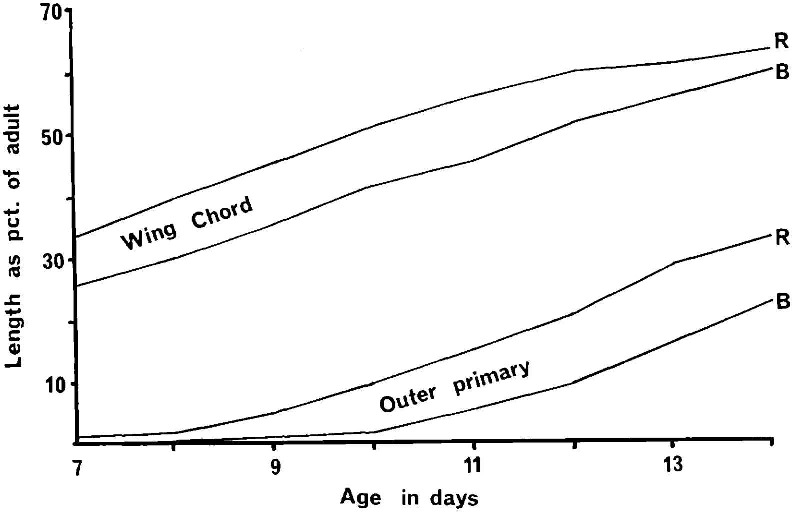

FIGURE 5. Wing chord and outer primary web lengths in the American Robin (R) and the Eastern Bluebird (B) during the second week of life, given as a percentage of the mean adult values (129.3 and 88.0 mm, 99.2 and 72.5 mm for the two species, respectively, with sample sizes as in Figure 3 for the robin and given in the text for the bluebird.

The foraging behavior characteristic of a species is known to be related to pre-fledging development. Ricklefs (1968) obtained lower values of R (<0.9) for species which, like the robin, forage on the ground. For species like the bluebird that glean and perch-feed, values tend to be greater than 0.9 but less than those for aerial feeders (> 1.1).

In summary, these results corroborate the findings of von Haartman (1957), who concluded that: (1) the rate of weight increase was similar in the Spotted and Pied flycatchers (*Muscicapa striata* and *M. hypoleuca*), although the hole-nesting Pied Flycatcher stays in the nest longer than the open-nesting Spotted Flycatcher; (2) the period of weight increase in the young of hole-nesters is only moderately prolonged; and (3) the period of remaining in the nest after attaining full weight is more adaptable to nest site location than the rate of weight increase.

Seasonal Weight Variation.—Peakall (1970) noted that the Eastern Bluebird is double-brooded throughout most of its range. In southern Michigan I found that "spring" nests are begun in April and early May. "Summer" nests are initiated from mid-June to late July and may or may not involve birds that have already reared one brood. An "intermediate" period (mid-May to early June) includes a small number of nests by adults that have not yet nested successfully and will not attempt a second nest if they are successful.

I found no difference in spring brood and summer brood weights for *S. sialis*. The average difference in the mean daily weights for the two nesting periods was only 0.4 g (SD = 0.4, maximum = 1.2 g), and daily weight maxima occurred with equal frequency in both periods (8 spring, 8 summer). The seven spring broods that were weighed, however, averaged 4.9 young/brood whereas the five summer broods averaged only 3.2 young/brood. Accordingly, two nests containing five young and with the same parents in the same nesting box during the spring and summer of 1970 showed a slight overall difference in the weights. The total sum of the daily mean nestling weights over the entire 16-day period was 305.5 g for the spring brood, and 292.6 g for the summer brood. Apparently more young can be reared per brood or the same number of young are better nourished in spring than in summer.

Diurnal Weight Variations.—Diurnal weight changes were examined in a brood of four 12-day-old young, the oldest of which was 1.5 days ahead of the youngest. Ambient temperature was constant (15° C), as was the food supply.

The average weight gain of the two oldest chicks was 0.35 g/hr during the first 4 hours after awakening. The corresponding figure for the two youngest chicks was 0.12 g/hr. In the following 6-hour interval the weight increments of the younger nestlings were greater (0.32 g/hr) than those of the older nestlings (0.24 g/hr). Little weight change was noted in any of the nestlings during the final 4 hours. If we assume that all the young are equally hungry when feeding commences in the morning, the smaller nestlings appear to be at a competitive disadvantage during the early feedings, but gain weight more rapidly later in the day when their older siblings are satiated.

These four young averaged an overnight weight loss of 1.21 g (0.12 g/hr), and this appeared to be independent of age or extent of development. The female did not brood during the observations. Overnight weight loss was recorded for another nest containing four 12-day-old young at similar temperatures and with the female also not brooding and the results were nearly identical. Weight loss was 1.0-1.3 g per nestling ($\bar{x}$ = 1.18 g), and for all eight nestlings the average weight loss amounted to 4.8% of the body weight of the previous night. A third nest with four 3-day-old young but with the female brooding averaged only a 0.14 g loss from a mean weight of 7.74 g. This lower figure (1.4%) for overnight weight loss indicates the importance of the brooding female in supplying heat (to reduce heat loss by the young) and humidity (to reduce water loss which, in turn, affects heat exchange). Other factors (e.g., the lower metabolism of younger nestlings) also tend to increase the observed difference whereas others (variations in feather insulation and in the body surface area to volume ratio) tend to decrease the difference.

Artificially Increased Broods

Lack (1948, 1949), Perrins (1965), and others have related clutch size with the maximum number of young that a species can raise. If this is true for *S. sialis,* we would expect that, within limits, an artificially increased brood of this species would develop slower than the rate of a normal brood (Fretwell et al., 1974). If this reduced rate is below the threshold needed for the maintenance and growth requirements, the brood would be reduced by mortality.

This hypothesis was tested during 1970 when two nests containing five and four young (the first in spring, the second during summer, both with normal-sized broods for those seasons) were increased to eight and seven young, respectively, by adding healthy young of the same size from nearby nests that were destroyed by predators. In both cases the results were similar (Table 4). On the last weighing before termination of the experiments by my removal of the young, the total weights of the artificially increased broods were greater than those of concurrent, normal-sized broods of the same age weighed elsewhere in the study area. The differences, however, were less than the minimum weights of individual young in normal broods (63.3—55.0 = 8.3 < 9.3, and 111.4—97.2 = 14.2 < 21.3). If food resources were uniformly distributed at these nests during the experiments, it appears that the young in average size broods (five and four young for spring and summer nestings, respectively) are better nourished and that average brood size may be related to the maximum number of young the adults can feed. Other factors, however, such as postfledging feeding and parental care or brooding capabilities of the female, undoubtedly also influence brood size.

TABLE 4.
Results of experiments involving artificially increased broods.[1]

Nestling weights (g) at conclusion	Experiment No. 1		Experiment No. 2	
	Normal	Increased	Normal	Increased
Mean	11.1	9.0	24.0	15.9
Maximum	12.6	9.3	27.5	20.2
Minimum	9.3	6.7	21.3	9.8
Total Weight of Brood	55.0	63.3	97.2	111.4

[1] Experiment 1: three young added to brood of five on day 0, concluded on day 4.
Experiment 2: three young added to brood of four on day 2, concluded on day 9.

SUMMARY

Development in the Eastern Bluebird was studied from 1970 to 1975 in southern Michigan. Body and plumage measurements indicate that the young of this species attain adult proportions at 35-40 days, i.e. when juveniles become independent of the parents. Nestlings of the same chronological age may be separated by as much as three days in stage of development.

Hatchling weight varies considerably and is positively correlated with the size of the egg. Growth in the cavity-nesting bluebird differs from other open-nesting New World thrushes, especially the American Robin, in that: (1) a greater percentage of the adult weight (90.7%) is attained before fledging; (2) a greater length of time (9.0 days) is required for attaining from 10% to 90% of the asymptotic weight; and (3) wing chord develops slower relative to the adult size, but is longer at the time of nest departure. The overall growth rate constant in the bluebird, however, is near that of the open-nesting species. These results appear to reflect a prolonging of the nestling period in the cavity-nesting Eastern Bluebird. Feeding methods employed by these species, however, may also be important.

Overnight weight loss was greater for young that were not brooded by the female (4.8% of the body weight) than for smaller young that were brooded (1.4%). Spring and summer broods exhibited no significant weight differences although summer broods had fewer young. Young hatched in summer left the nest at an earlier age than did young hatched in spring.

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