

BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. 42, No. 1

JANUARY 1971

PAGES 1-78

GROWTH AND CALCULATION OF AGE FOR RED-WINGED BLACKBIRD NESTLINGS

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The Red-winged Blackbird (*Agelaius phoeniceus*) is a highly successful icterid that maintains large population numbers, perhaps through its ability to nest in marshes, weed fields, agricultural legumes, and second-growth vegetation. Case and Hewitt (1963) report no difference in nest success of redwings in different types of habitats.

We undertook this study (1) to determine mean growth and relative growth rate of several different body parts of nestlings, including feathers, (2) to develop a method of determining their ages with a reasonable degree of accuracy, and (3) to find if any differences exist between the growth of nestling redwings raised in a marsh and those in upland habitat. Redwing eggs hatch asynchronously, with as much as 48 hours between hatching of the first and last eggs in a clutch. Consequently we also wanted to learn whether the growth rate of the nestlings depends on the hatching sequence, on the number of birds in the nest, or whether it is independent of these factors.

Mean growth in weight of Red-winged Blackbird nestlings in marshes has been reported by Williams (1940) and Brenner (1964). Williams gave mean tarsal growth; both he and Nero (1961) showed methods of sexing redwing nestlings of known age. No one has given methods of determining age of nestling redwings.

METHODS AND PROCEDURES

We studied Red-winged Blackbirds nestlings around a small lake at Battle Creek, Michigan in 1965. Cattails (*Typha* spp.) were the predominant vegetation near the edge of the lake, with open meadows and scattered dogwood (*Cornus* spp.) and willow (*Salix* spp.) beyond them. We studied nestlings at Toledo, Ohio in 1964 and 1965 in an upland habitat of old weed fields, ditch banks and second-growth vegetation.

We visited nests at least once each day, to record the weights and measurements nearly the same time each day. We marked nestlings in the sequence of hatching by placing nail polish on their claws (claw 1, 2, etc.). New polish was added to the claw at regular intervals to insure proper identification of individual nestlings. We weighed nestlings to the nearest one-tenth gram on

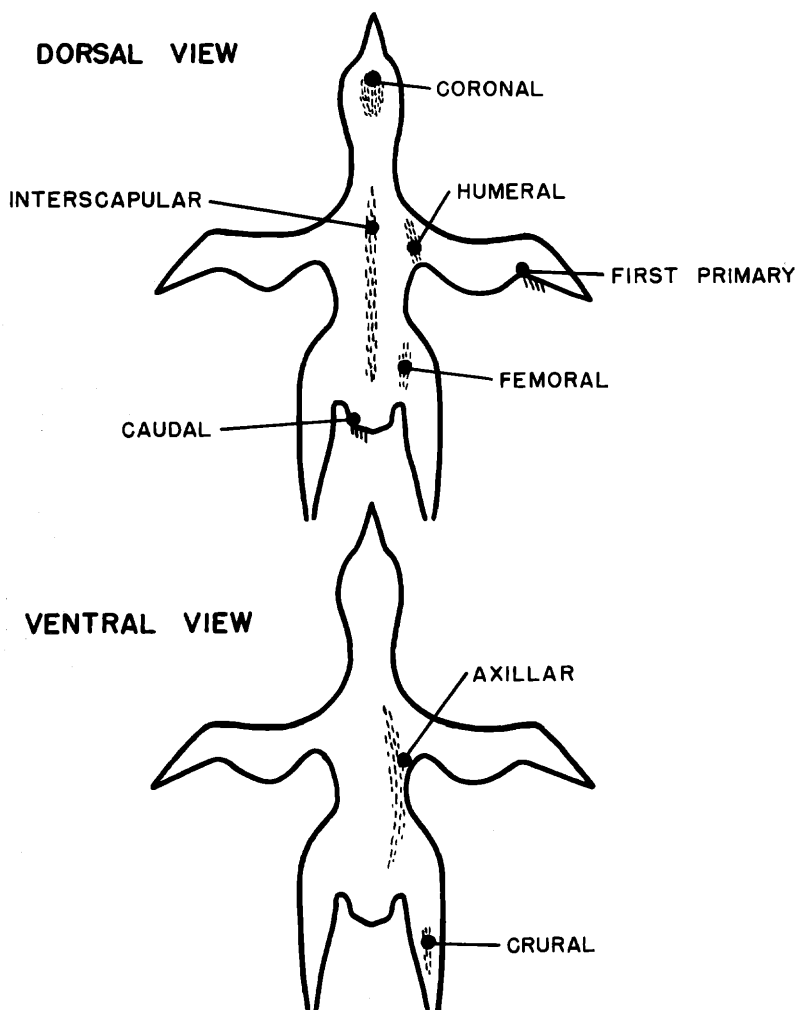


Figure 1. — Regions on redwing nestlings where feathers were measured.

a double-beam balance after they had been handled sufficiently to cause voiding of wastes.

Redwings hatch with the eyes closed. As they grew, we recorded, using arbitrary values, whether the eyes were closed (0), cracking open (1), half-open (2) or fully open (4). Measurements of growth were made with calipers and millimeter rulers on the following parts of nestlings to determine mean growth and instantaneous relative growth: *toe span*, distance from the tip of toe one to the

tip of toe three when extended (including claws), nearest mm; *total body length*, distance from the tip of the culmen to the tip of the tail (including rectrices when present), nearest mm; *tarsus*, nearest one-half mm; *wing*, distance from the last bend in the wing (radiale region) to the tip of phalanges (before feathers were present) and to the tip of primary eight after it emerged (wing chord), nearest mm; *mandibular tomium*, distance from the tip of the lower mandible to the commissural point, nearest mm; *mandible tip (culmen) to nostril opening*, distance from the anterior tip of the culmen to the anterior edge of the nostril opening, nearest one-half mm; and *gape width*, distance across the base of head from one commissural point to the other, nearest one-half mm.

Examination of the eight feather tract regions took place each day. If one feather capsule had pushed through the epidermis it was recorded as *projecting*. After the feather capsules had projected, we examined them daily, to determine when the capsule was broken exposing feather barbs. We called this *fringing* (un-sheathing) of the feather sheath.

We measured an individual feather from certain tracts each day after projection occurred. In most tracts we could not be sure that the same feather was measured each day. The feathers were so similar in length in an area that the choice of different feathers should affect the mean values very little. We measured a feather from each of the following tracts to the nearest mm: *caudal*, left outermost rectrix; *alar*, first (most proximal) primary (left wing); *humeral*, the longest feather (usually found in the middle of the tract running parallel to the long axis of the body); *capital*, feather in center of the coronal region; *spinal*, longest feather in the interscapular region; *ventral*, longest feather in the axillar region; *crural*, longest feather in the mid-portion of the anterior side of the leg; *femoral*, longest feather in the mid-portion.

Wetherbee (1957) describes the regions (Figure 1) from which we measured feathers.

The number of specimens represented in this study is greater than has been reported previously on any passerine bird. These large numbers make any interpretation of growth more valid. We also measured more body components than represented in previous studies on bird growth. Consequently, we took advantage of the data and of a computer to perform several calculations.

We calculated the mean, standard error and instantaneous relative growth rate for each of the growing body components. We obtained the correlation coefficients for each growth component compared with age in days. We chose the characteristics that appeared to correlate best with age and ran a step-wise regression routine to select the best criteria for predicting the age of nestlings.

We also computed the *b* (regression coefficient) values for the slope of the growth curves for the different groups of nestlings and tested the difference between these values by using Student's *t*-test.

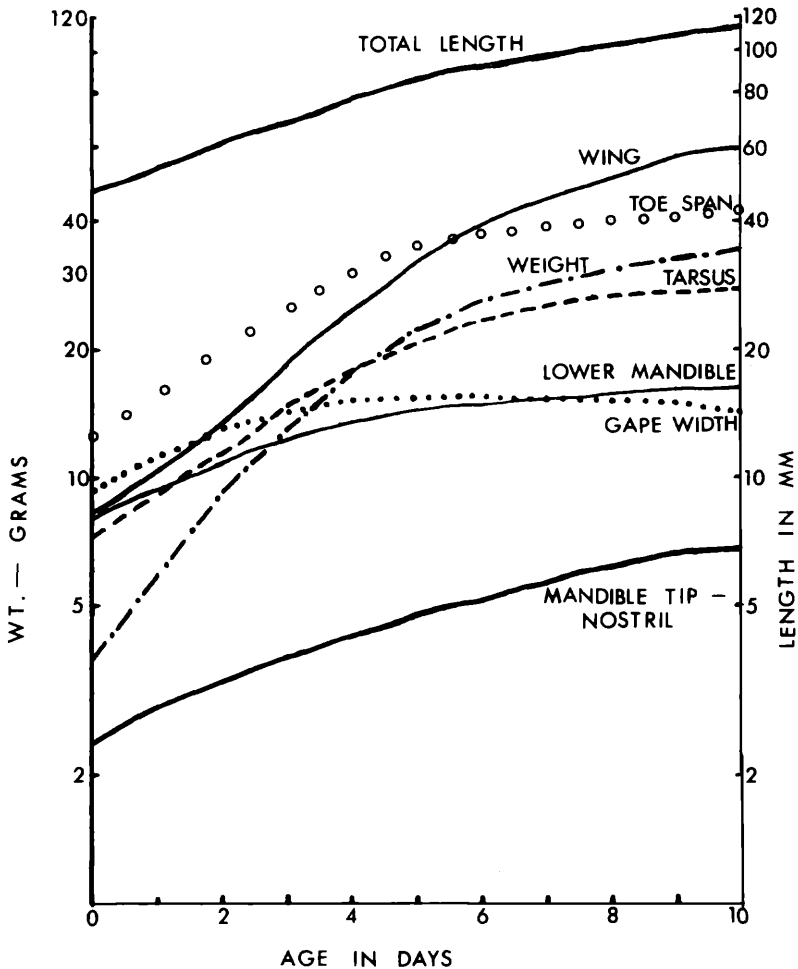


Figure 2. — Growth in weight, and increase in length of different parts, in redwing nestlings; semilogarithmic. Means are plotted for weights of 182 nestlings on day 0, to 44 on day 10; on other body components, the numbers ranged from 85 on day 0 to 25 on day 10.

RESULTS AND DISCUSSION

Neosoptiles on feather tracts, appearance of young. Of the 190 newly-hatched nestlings we examined, 180 had down on all eight tracts, 10 had no down on the crural tract. The position in the hatching sequence of 8 of these 10 nestlings was: 2 from egg one; 1, egg two; 1, egg three; 4, egg four. Saunders (1956) and Wetherbee (1961) describe neosoptiles on all eight major feather tracts in

redwing nestlings. Clark (1967) found a distinct variation in presence and absence of down in the interscapular region of nestling redwings. He pointed out the intraspecific variation in passerine natal pterylosis and possible seasonal variation.

Saunders (1956) describes the skin as salmon-pink in newly-hatched redwing nestlings. We agree with this description in some instances, but usually they appear more orange than pink. Wetherbee and Wetherbee (1961) describe newly hatched redwings as orange. The orange color is probably xanthophyll derived from phytophagous insect larvae.

An egg tooth on the upper mandible was often visible but almost gone by day 8.

Mean growth and growth rates in weight. Figure 2 illustrates the growth in weight and body parts of all the redwing nestlings. This figure plots mean growth data semilogarithmically; if growth were logarithmic over the entire nestling period the growth curves should be straight lines. As they are not straight lines (total length shows the closest approximation) we calculated the growth rate (R) by the method used by Banks (1959) when growth is nonlogarithmic. This is:

$$R = \frac{2.3 \log W_2 - \log W_1}{T_2 - T_1}$$

(2.3 being a factor to convert logarithms to the base 10 to natural logarithms).

This figure is valid for comparisons only if we assume that growth during any one day is logarithmic even though over the entire nestling period it is not. In this formula, W_1 is the weight (or other measurement) at T_1 , and W_2 is the weight (or other measurement) at a later time, T_2 .

Table 1 shows the mean weight increases and the growth rate (R) of all redwing nestlings. Growth is rapid in the first few days, the rate declining in the last few days in the nest. The values are similar to those presented by Banks (1959) for the White-crowned Sparrow (*Zonotrichia leucophrys*) and by Dawson and Evans (1957, 1960) for the Field Sparrow (*Spizella pusilla*), Chipping Sparrow (*Spizella passerina*), and Vesper Sparrow (*Pooecetes gramineus*), and by Maher (1964) for the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*). The rates of growth for sparrows drop off faster than for the redwing. This is to be expected as they leave the nest in fewer days, attaining a relatively greater proportion of adult size faster than redwings.

Comparisons of mean growth and growth rates in weight and body parts in marsh and upland nesting redwings. The calculated b values for the slopes of the growth curves for weight of the marsh and upland nestlings were not different ($P > 0.05$, using a 2-sided Students' t-test). A simple index was calculated (not to be confused with the index shown by Banks (1959)) by taking the mean of the

TABLE 1. REDWINGED BLACKBIRD NESTLING GROWTH IN WEIGHT — GRAMS

Day	N	Mean weight	Range	Mean instantaneous growth rate (R)
0	182	3.8 ± 0.1	2.5- 5.8	
1	171	5.9 ± 0.1	2.4- 9.5	0.44
2	164	9.3 ± 0.1	5.6-13.7	0.44
3	153	13.1 ± 0.2	7.9-18.1	0.34
4	131	17.7 ± 0.2	11.5-25.3	0.30
5	133	22.3 ± 0.3	14.0-31.0	0.23
6	120	26.1 ± 0.3	18.1-36.4	0.16
7	118	28.6 ± 0.4	19.5-37.9	0.09
8	101	30.7 ± 0.5	17.0-40.5	0.07
9	75	32.8 ± 0.7	24.1-48.1	0.07
10	44	34.3 ± 1.0	25.0-43.0	0.04
11	7	37.1	29.2-40.9	

R values over the entire nestling period for weights and other measurements in the marsh and upland nestlings. We found no differences in the mean growth rates in weight or body parts of growing nestlings in the two types of nesting habitats. Williams (1940) reported sexual differences in weight increase of redwing nestlings. We estimate that nearly equal numbers of males and females hatched from all the eggs in our study. Of 95 fledglings produced, 41 were males and 54 were females. We found a difference in weight increase between males and females but not in any of the other parameters measured (to be reported elsewhere). The growth rate index of females in both the marsh and upland was 0.20 through day 10 with mean weights on day 10 of 30.7 ± 0.9 g for 6 marsh birds and 27.7 ± 0.5 g for 11 upland birds. The growth rate index for males in the marsh was 0.23 and in the upland 0.24 through day 10. Six marsh males weighed 40.2 ± 0.9 g and 12 upland males weighed 36.8 ± 1.1 g on day 10. The birds in the marsh population weighed a little more at fledging, but the indexes for rate of growth are not different. Therefore, the values for weight increase and body parts were combined from the two study areas regardless of sex. The data shown in Tables 1 and 2 are based on combined data. Table 1 shows the rate of weight increase; Table 3 shows the rate of growth in length of body parts. Rate of growth is rapid at first for each body component and then declines. Gape width was the only portion of the body to decline in size after day 6. This was due to a reduction in the fleshy rectal portion.

The mean rate of growth (index) shown in Table 3 is slower for head parts and total length than for toe span, tarsus length and wing length. The head parts and total length do not triple their original size whereas the toe span increases by 3.5X, the wing 7X,

TABLE 2. REDWING NESTLING MEAN GROWTH IN MM

Day	N	Lower mandible	Mandible tip to nostril	Gape width	Toe span	Wing length	Total length	Tarsus length
0	85	7.8 ± 0.1	2.4	9.2 ± 0.1	12.8 ± 0.1	8.2 ± 0.1	47.6 ± 0.2	7.3 ± 0.1
1	80	9.3 ± 0.1	2.9	11.0 ± 0.1	15.9 ± 0.2	10.0 ± 0.1	53.8 ± 0.3	9.0 ± 0.1
2	83	10.9 ± 0.1	3.3	13.0 ± 0.1	20.3 ± 0.2	13.2 ± 0.2	61.6 ± 0.4	11.4 ± 0.1
3	76	12.4 ± 0.1	3.8	14.1 ± 0.1	25.3 ± 0.2	18.1 ± 0.3	69.4 ± 0.4	14.6 ± 0.2
4	71	13.5 ± 0.1	4.2	14.9 ± 0.1	30.5 ± 0.3	24.8 ± 0.5	77.7 ± 0.5	17.8 ± 0.2
5	77	14.4 ± 0.1	4.7 ± 0.1	15.2 ± 0.1	34.9 ± 0.2	33.0 ± 0.4	85.6 ± 0.4	20.8 ± 0.2
6	71	14.8 ± 0.1	5.0 ± 0.1	15.4 ± 0.1	37.3 ± 0.3	39.7 ± 0.4	91.5 ± 0.5	23.4 ± 0.2
7	63	15.3 ± 0.1	5.6 ± 0.1	15.1 ± 0.2	39.4 ± 0.3	45.2 ± 0.5	97.7 ± 0.8	25.1 ± 0.2
8	48	15.7 ± 0.1	6.1 ± 0.1	14.8 ± 0.2	40.7 ± 0.3	50.3 ± 0.5	103.3 ± 0.7	26.2 ± 0.2
9	39	16.1 ± 0.1	6.4 ± 0.1	14.7 ± 0.1	41.7 ± 0.4	54.7 ± 0.6	109.3 ± 0.8	26.7 ± 0.2
10	25	16.4 ± 0.2	6.8 ± 0.1	14.3 ± 0.2	42.7 ± 0.6	58.2 ± 0.9	113.3 ± 1.0	27.6 ± 0.4

TABLE 3. REDWING NESTLING MEAN INSTANTANEOUS GROWTH RATE (R)

Day	N	Lower mandible	Mandible tip to nostril	Gape width	Toe span	Wing length	Total length	Tarsus length
1	80	0.17	0.15	0.18	0.22	0.22	0.12	0.23
2	83	0.16	0.14	0.15	0.25	0.25	0.14	0.23
3	76	0.13	0.15	0.10	0.22	0.32	0.13	0.25
4	71	0.09	0.12	0.05	0.19	0.32	0.13	0.20
5	77	0.06	0.11	0.01	0.14	0.28	0.09	0.15
6	71	0.04	0.08	0.02	0.07	0.19	0.05	0.12
7	63	0.03	0.08	-0.01	0.05	0.13	0.07	0.07
8	48	0.02	0.09	-0.01	0.03	0.11	0.04	0.05
9	39	0.02	0.06	-0.01	0.03	0.13	0.06	0.02
10	25	0.03	0.04	-0.05	0.04	0.08	0.05	0.03
Index		0.08	0.10	0.04	0.12	0.20	0.09	0.14

TABLE 4. PROJECTION AND FRINGING OF FEATHER TRACTS IN REDWING NESTLINGS (1965) IN PER CENT OF INDIVIDUALS WHERE IT HAS OCCURRED¹

Day	N	Caudal		Alar		Humeral		Capital		Ventral		Spinal		Cruial		Femoral	
		P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F
1	80																
2	83					48						1					
3	76			100		70				41		39		3			26
4	71	25		100		100		14		97		96		72			96
5	77	75		100	19	100	8	61		100	13	100		99			100
6	71	100	8	100	92	100	76	100		100	82	100		100	31	100	42
7	63		46		100		100		22		100						92
8	48		94		100		100		83		100						100
9	39		97		100		100		97		100						100
10	25		100		100		100		100		100						100

¹These data are from nestlings where all the characteristics were recorded for that day. P, Projection; F, Fringing.

and the tarsus almost 4X. The head parts and total length are larger in proportion to the total body size at hatching than the toe span, wing, or tarsus, reflecting the rapid development of brain and eyes on the long axis of the body. The mouth parts must be large enough to serve as a feeding target for the adult and the total length contributes to the nestling's ability to reach food. The tarsi must grow rapidly for support, the toes as tools for supporting and grasping and the wings for flight by the time the nestlings fledge.

It is important to mention that several young in nests of four or five died of starvation in the upland population at Toledo. Those which died were always nestlings which hatched last, growing thin and dying in the early days of development. In five nests of four nestlings each, a fourth-hatched nestling died of starvation on day 1, 5, 6, 8, and 9 respectively. Three last-hatched nestlings in nests of five died of starvation; one died on day 1 and two on day 4. Food may have been scarce, especially in June of 1964 when there was very little precipitation at Toledo. Brood reduction was taking place in our study in the upland. The gape width did not increase in size after day 6 in most nestlings. Differences in size of gape before day 6 were common. This may result in less feeding for smaller young having a small gape. No nestlings starved at the Battle Creek marsh, perhaps because food was more plentiful.

Lack (1947, 1954, 1966) reported that, in species of birds that have asynchronous hatching, brood size may be adjusted to food availability. In times of food shortage, the oldest and largest nestlings are fed at the expense of smaller and weaker ones, insuring that at least some of the nestlings will survive. Ricklefs (1965) demonstrated this in the Curve-billed Thrasher (*Toxostoma curvirostre*), describing two possibilities of adjusting brood size: 1) prior evaluation of food availability and reduction of clutch size or 2) brood reduction after hatching when the food fluctuations are unpredictable.

Orians (1966) found that lakes of higher conductivity produced more food for Red-winged and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) than lakes of low conductivity. He found no yellowheads breeding on lakes with conductivities less than 1100 micromhos/cm while redwings nested on lakes with conductivities as low as 625 micromhos/cm. He explained that the smaller size of the redwing resulted in less food demand, permitting the redwing to breed on lakes of lower productivity. Orians also found strong evidence that nestling yellowheads received less food on lakes with lower conductivity values. Willson (1966) reported marked brood reduction in nestling yellowheads under adverse environmental conditions.

Brenner (1966) reported the influence of drought on reproduction in redwings. With less precipitation, the mean standing crop of insects decreased and the number of breeding females decreased in 1962 and 1963. When the precipitation increased in 1964, the mean standing crop of insects was elevated and there were more breeding

TABLE 5. REDWING FEATHER TRACT MEAN (NEAREST 0.5 MM) GROWTH IN MM

Day	N	Caudal	Alar	Humeral	Capital	Ventral	Spinal	Cruural	Femoral
3	76		3.5	1.0		0.5	0.5		0.5
4	71	0.5	9.0 ± 0.5	2.5		1.5	1.5	0.5	1.5
5	77	1.0	15.5 ± 0.5	5.0	0.5	3.5	3.5	1.5	3.0
6	71	2.0	22.5 ± 0.5	8.0	1.5	6.0	6.0	3.0	5.5
7	63	4.0	28.5 ± 0.5	11.0 ± 0.5	2.5	9.0 ± 0.5	9.0	4.0	8.5
8	48	6.5 ± 0.5	34.5 ± 0.5	13.5 ± 0.5	4.0	11.5 ± 0.5	12.0	5.0	10.5 ± 0.5
9	39	9.0 ± 0.5	40.0 ± 0.5	16.5 ± 0.5	5.0	14.5 ± 0.5	14.5 ± 0.5	6.0	13.0 ± 0.5
10	25	11.5 ± 0.5	44.0 ± 0.5	19.0 ± 0.5	5.5	17.5 ± 0.5	17.0 ± 0.5	6.5	15.5 ± 0.5

TABLE 6. REDWING FEATHER TRACT MEAN GROWTH RATES (R)

Day	N	Caudal	Alar	Humeral	Capital	Ventral	Spinal	Cruural	Femoral
3	76		1.23						
4	71		0.89	1.08		1.24	1.29		1.67
5	77	1.30	0.54	0.77	1.52	0.86	0.85	0.79	0.82
6	71	0.80	0.38	0.47	0.85	0.58	0.64	0.56	0.58
7	63	0.68	0.24	0.31	0.57	0.40	0.37	0.32	0.40
8	48	0.46	0.19	0.22	0.38	0.26	0.28	0.21	0.24
9	39	0.37	0.15	0.21	0.25	0.23	0.19	0.19	0.22
10	25	0.22	0.09	0.12	0.14	0.17	0.17	0.15	0.16
Index (First 6 Days)		0.64	0.58	0.51	0.62	0.60	0.60	0.37	0.68

females. Mean values for weights of nestlings reported by Brenner (1964) were lower when compared to those of our nestlings and of Williams (1940). This may be because of scarcity of insects to feed nestlings (Brenner suspects this may be true, *pers. comm.*).

Projection, fringing and growth of feathers. Table 4 gives the percentage of nestlings having feather capsules projecting from the epidermis or fringing on the ends. The alar and humeral tracts are the first to project. Ventral, spinal, and femoral tracts project prior to the caudal, capital, and crural tracts. Fringing occurs earliest on the alar, humeral, and ventral tracts. The spinal, femoral, and crural tracts fringe before the caudal and capital tracts. The ventral tract probably fringes somewhat earlier than the spinal because of its contact with the nest. Allen (1914) reported that alar feather sheaths began projecting on day 2 and were breaking open on day 6.

Table 5 gives the mean growth of feathers; Figure 3 shows that growth of feathers is not logarithmic throughout the nestling period. Table 6 gives the growth rates of the different feather tracts. The index of growth rate for the first 6 days shows that most tracts grow at about the same rate except for the crural tract. The rate of growth in feathers appear to be much more rapid than the body components measured.

Defecation behavior. We recorded the occurrence of defecation in all the nestlings. The per cent of birds voiding wastes at least once when nests were visited was about 2 per cent on day 0 and increased in the following 7 days to 3, 10, 38, 68, 82, 91, and 97 per cent, and then remained about the same until fledging. We found no difference in the mean per cent of nestlings voiding wastes in the marsh and upland.

The rate of defecation increased with age. This probably does not indicate the quantity of food the nestlings receive as their ability to store more food would increase with size. Although they receive more food as they grow, their rate of weight gain over the previous day is greater when they are younger. From day 2 through 6 the per cent of birds defecating becomes progressively higher each day. The greatest amount of tissue is being added then. After day 8 when the amount of tissue added each day is reduced, the defecation rate remains high. Perhaps this is related to a behavioral disturbance as they become aware of danger at older stages. Other factors may be utilization of food by the digestive tract and differential production of uriniferous wastes.

Eye opening in nestlings. The time of eye opening was recorded for all the nestlings. Between days 3 and 4, the eyes of redwing nestlings begin to open. Between days 4 and 5 the eyes become half open and all are fully open by day 7. Mean values for eye opening at the arbitrary values of 0 (not open), 1 (cracking open), 2 (half open), and 4 (open) were: day 2, 0.07; day 3, 0.61; day 4, 1.46; day 5, 2.61; day 6, 3.58; day 7, 4.0. Until the eyes open in nidicolous birds, they are dependent on the auditory and mechani-

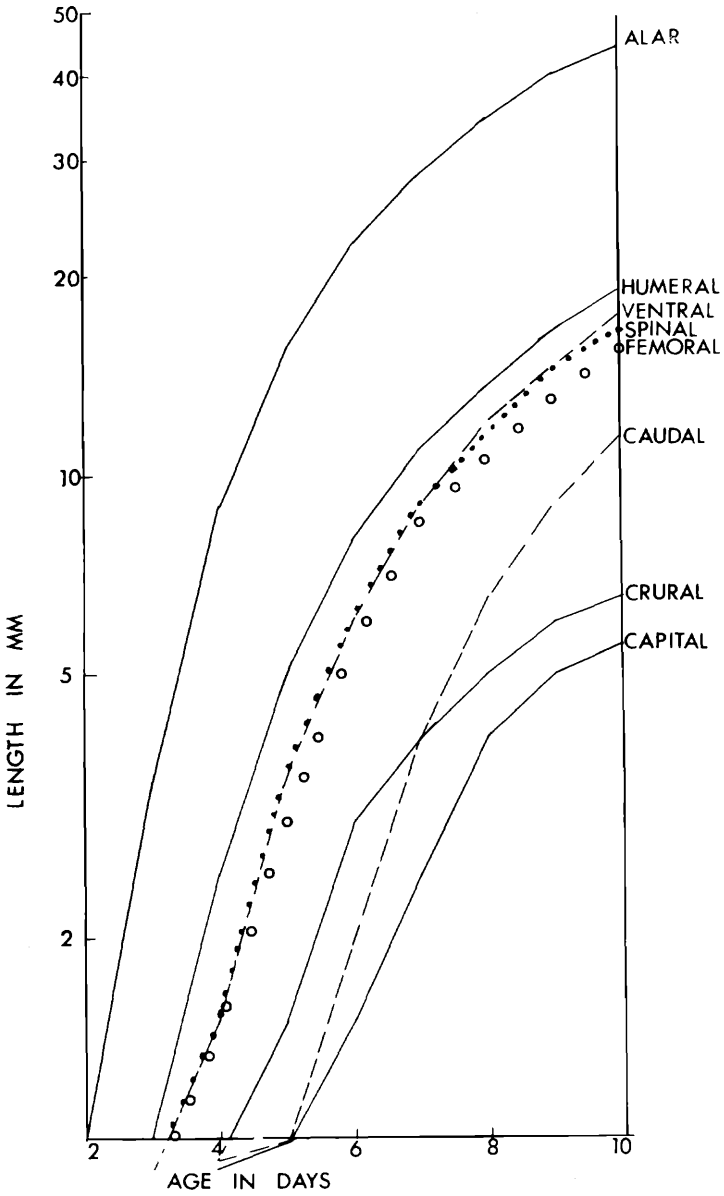


Figure 3. — Growth in length of feathers in redwing nestlings; semilogarithmic. Numbers ranged from 83 on day 2, to 25 on day 10.

cal (touch) senses. Burns (1921) reviewed the time of eye opening in several species of birds but did not state whether they were partly or fully open. Since the acquisition of sight changes the behavior of the nestling, this should be of utmost importance to any biologist working with nestling birds. Fautin (1941) found the eyes of Yellow-headed Blackbirds opening by day 3.

Calculation of nestling age. Table 4 shows that if the alar tract projects, most of the birds are at least 2 days old and if the capital tract projects most of the birds are at least 5 days old. Furthermore, if the alar tract is fringing, most nestlings will be at least 6 days old and if the capital tract is fringing they are at least 7 days old. These criteria may be of special value to investigators wishing to know the minimum age of nestling redwings. Horwich (1966) used feather development as a means of determining the age in young Mockingbirds (*Mimus polyglottos*) and found it reliable. Some features such as length of wing, mandibular tomium, mandible tip to nostril opening, and some feather tracts change so slowly that marked differences do not occur and considerable overlap in range values exist from one day to the next. A feature such as toe span is difficult to measure and the toes can be easily injured.

Total length is the best body component for determining age because of rapid increments in growth. Other growth features selected as good age criteria were projection and growth of the alar tract and growth of the spinal tract. Alar projection was uniform and the first primary grew rapidly (Table 5). We found little variation between birds, in growth of the spinal tract.

We used a computer in a stepwise-regression routine to select from 35 variables those most reliable for predicting age. This routine selects growth components that correlate best with age, and arranges them in the order of selection, showing a constant and regression coefficient. The resulting equation was:

$$\text{Age (in days)} = 2.56 + 0.06 \text{ total length} + 0.90 \text{ alar projection} \\ (0 \text{ if not projecting, } 1 \text{ if projecting}) + 0.08 \text{ first primary} \\ \text{length (if present)} + 0.06 \text{ spinal feather length (if present).}$$

If no feathers are present, only the total length needs to be taken.

The standard error of estimate was 0.45 which means that most predictions of age will be within 1 day of the correct age. A value for alar projection is zero if no feathers are present, and a value of one if present. For instance, if a nestling is 116 mm in total length, alar tract projecting (1), first primary 41 mm, and the longest spinal feather in the interscapular region is 16 mm, the age would be:

$$\text{Age} = -2.56 + 0.06 (116) + 0.90 (1) + 0.08 (41) + 0.06 \\ (16) = 9.54 \text{ days.}$$

The projection and fringing of feather tracts shown in Table 4 does aid in calculating age with more accuracy. For instance, if

a nestling is 85 mm in total length, alar tract projecting, primary one 27 mm in length, and spinal feather 6 mm in length, the formula gives a value of 5.96 days. We might accept this value if the capital tract is not fringing. If it is fringing the nestling is probably at least 7 days of age and since our formula should be accurate to within 1 day most of the time, the nestling is probably 7 days of age.

Another example of more precise age determination is a younger nestling with a value of 2.56 obtained when total length is 66 mm, alar tract projecting, primary one 2.5 mm long, and no growth on the spinal tract. If this nestling has no ventral tract projecting it is not 3 days old, but if the humeral tract is present, it is at least 2 days of age.

Effect of number of siblings and hatching sequence on growth.

As there are no significant differences in increase of weight in nestlings from marsh or upland breeding birds we combined all the data from the two population samples.

We calculated the mean increase in weight and growth rate for nestlings one, two, three, and four for all nestlings regardless of the number in the nest. We found no differences in the growth rates. The differences in the b values for the slopes of the growth curves were not significant ($P > 0.05$). The data showed that nestlings from nests containing different numbers of siblings did not grow at different rates. Therefore, regardless of the size of the brood, all nestlings were receiving about the same quantity of food. The last-hatched nestlings in nests of four or five may die because of starvation. This usually happens by day 6, before there would be any distinct differences in size of the sexes. It is unlikely that sex has any influence on brood reduction. Willson (1966) reported that although nestling male Yellow-headed Blackbirds grow faster than females, younger males do not become larger than older females until age 5-7 days.

The mean increase and growth rate in weight of nestlings from nests with different numbers of siblings showed no differences. We found no significant differences in the b values for the slopes of the growth curves ($P > 0.05$).

Environmental variables influencing the amount of food available for nestlings are always present, and there is variation in the frequency of feeding. Thus, fluctuations in mean growth rate for each day are expected. Therefore, we calculated as an index, (not the same as calculated by Banks, 1959) the mean of the growth rates for the nestling period. For nests with one or two, three, or four nestlings, the indices were 24, 23, and 24, respectively, for the initial 9 days. For first, second, third, or fourth hatched nestlings, the indices were all 26 for the initial 8 days. In other words, no real differences existed in growth rate related to the number of birds in the nest or to the sequence of hatching. These figures do not include mean weights for those individuals that starved.

Paynter (1954) and Lack and Silva (1948) found small differences in mean growth in weight of broods of different sizes in Tree

Swallows (*Iridoprocne bicolor*) and the European Robin (*Erithacus rubecula*) respectively, but the differences were not significant. Lack (1947, 1954, 1966) discussed in detail the significance of clutch size and showed from his own data and data of others, that broods containing fewer young often have a greater mean increase each day and weigh more at fledging than broods having more individuals. This is especially pronounced for passerine species that lay many eggs (e.g. the Great Tit (*Parus major*)).

ACKNOWLEDGMENTS

We would like to express appreciation for the aid given by The University of Toledo; Midland College, Fremont, Nebraska; The Ohio Agricultural Research and Development Center; and Battle Creek Community College, Battle Creek, Michigan. We thank C. Richard Weaver for planning of statistical evaluations and computer programming. Richard V. Andrews, Robert W. Belknap, and especially Richard C. Banks and Julian Baumel made many helpful suggestions on a later version of the manuscript.

SUMMARY

The biology of growth of the Red-winged Blackbird (*Agelaius phoeniceus*) was studied at Toledo, Ohio in an upland habitat in 1964 and 1965 and at Battle Creek, Michigan in a marsh habitat in 1965. Nestlings were weighed and measured each day and a record was made of eye opening, defecation, presence of neossoptiles and projection, fringing, and growth of eight major feather tracts. Down was usually present at hatching on all feather tracts. Nestlings usually were an orange color at hatching.

Growth was not logarithmic over the entire nestling period in any of the characteristics measured. Mean growth increments and growth rate were similar in nestlings raised in marsh and upland habitats. There was some brood reduction in the upland nests but none in the marshes.

Time of feather projection is given for eight tracts. The alar tract is the first to project and fringe and the capital tract is last.

The per cent of nestlings that defecate when handled increases with age and is similar for marsh and upland birds. Eyes begin opening on day 3 and are fully open by day 7.

A formula for calculating age was developed that predicts age most of the time within one day of the correct age. It is: Age = $-2.56 + 0.06$ total body length + 0.90 alar projection (0, if not present; 1 if present) + 0.08 first primary length (if present) + 0.06 spinal feather length (if present). If feathers are not present only the total length need be measured.

There were no differences in mean growth increment or mean relative growth rate for first-, second-, third-, or fourth-hatched nestlings or in nests containing different numbers of siblings.

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Received July, 1970.