RED-WINGED BLACKBIRD NESTLING GROWTH COMPARED TO ADULT SIZE AND DIFFERENTIAL DEVELOPMENT OF STRUCTURES¹

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ABSTRACT

Red-winged Blackbirds (*Agelaius phoeniceus*) were studied at Toledo, Ohio, in an upland habitat in 1964 and 1965, and at Battle Creck, Michigan, in a marsh habitat in 1965. Nestlings were weighed and measured each day. In 1966 at Wooster, Ohio, adults were weighed and measured to obtain figures for comparison with nestling sizes at different stages in nest life.

Mean weight of 18 neonates was 3.19 g, which was 7.5 percent of 18 adult female weights (41.6 g) and 79 percent of 18 fresh egg weights (4.02 g). Male nestlings showed higher values for mean weight and mean length of other body parts than females, but females reached a greater percent of adult size faster than males.

All mean body weights and measurements increased in absolute size from hatching until day 10 except for gape width, which reached maximum size on day six and then decreased in width. The differential increase of size in different body parts shows a distinct correlation with their function while in the nest; those which were used during nest life developed in the first five days and those required after fledging developed in the last five days.

Rapid growth in weight occurred before rapid feather growth. Reduction in increases of weight each day is probably due to expenditure of more energy for feather growth and for maintenance of endothermy. The same phenomena are shown for many other species.

INTRODUCTION

Nice (1943) reviewed relative weight of neonates and of nestlings 10 days old, compared with adult weight. Wetherbee (1961) reported that the neonate redwing has very small bone size (expressed as percent of adult size), when compared with most other passerine species. He suggested that the redwings' delayed sexual maturity may be relevant in a consideration of slower developmental rate (proportional to incubation period of its embryos).

The purpose of this study was to determine how fast different parts of the bodies of young Red-winged Blackbirds (*Agelaius phoeniceus*) grow, compared to those of adults, data similar to, but more extensive than those of Nice (1943). In addition, an attempt was made to explain differences in rate of growth of different body parts based upon the function of these body components while birds were in the nest.

METHODS AND PROCEDURES

Redwings were studied in 1965 at Battle Creek, Michigan, where they nested around a small lake where cattails (Typha spp.) were the dominant form of vegetation, with open meadows with scattered dogwood (*Cornus* spp.) and willow (*Salix* spp.) beyond the cattails. Nestlings were studied at Toledo, Ohio, in 1964 and 1965, in an upland habitat of old weed fields, ditch banks, and second-growth vegetation. Further details are reported by Holcomb and Twiest (1968).

The nests were visited at least once each day and weights and measurements of nestlings were recorded at nearly the same time each day. Weight was obtained to the nearest one-tenth gram on a double-beam balance after the nestling had been handled sufficiently to cause voiding of wastes.

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Measurements of growth were made on parts of nestlings by means of calipers and rulers. The measurements described in this paper are:

- toe span—distance from the tip of toe one to the tip of toe three when extended, measured to the nearest mm
- total body length—distance from the anterior tip of the culmen to the tip of the tail (including rectrices when present), measured to the nearest mm
- tarsus, measured to the 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), measured to the nearest mm
- mandibular tomium—distance from the anterior tip of the lower mandible to the commissural point, measured to the nearest mm
- mandible tip to nostril opening, i.e. distance from the anterior tip of the culmen to the anterior edge of the nostril opening, measured to the nearest onehalf mm
- gape width—distance across the base of head from one commissural point to the other, measured to the nearest one-half mm

first (innermost) primary, measured to the nearest mm

Weights and measurements were taken from adult and immature female and male redwings at Wooster, Ohio, in October, 1966, and from other published sources giving weights and measurements of redwings.

RESULTS

Mean Weights and Measurements of Adult and Immature Male and Female Redwings

Eighteen male (five adult and 13 immature) and 12 female (eight adult and four immature) redwings were weighed and measured in October, 1966, at Wooster, Ohio. Immature and adult females had mean weights of 41.8 and 43.5 grams,

Characteristic	Ν	Males	Ν	Females
Total Length	51	231.3	35	198.7
Tarsus	18	29.0	12	26.4
Wing Chord	112	121.1	81	100.4
Lower Mandibular Tomium	18	22.7	12	20.2
First Primary	18	81.3	12	67.0

 TABLE 1

 Mean lengths of different morphological regions in adult redwings

respectively, while immature and adult males had mean weights of 58.3 and 66.4 grams, respectively. All other measurements on immatures and adults were so nearly the same that values were combined. Mean values for comparison of adult sizes with mean sizes of nestlings on different days were calculated by combining all of the data from the Wooster, Ohio, birds and from those presented by Selander and Kuich (1963), Stewart (1937), Meanley (1964), Howell and Van Rossem (1928), Norris and Johnston (1958), and Snyder and Lapworth (1953), and are shown in table 1. Altogether, 88 immature and 46 adult males had mean weights of 60.0 and 70.5 g, respectively. Sixty-six immature and 18 adult females had mean weights of 43.8 and 41.6 g, respectively. Because the immature females had already attained adult weight, they were included in the percent of adult weight column in table 2.

No. 6

Weights of Neonate Redwings Compared to Egg Weights and Adult Female Weights—Comparisons with other Icterids

The mean weights of nestlings on day 0, given in table 2, are not all weights of neonates. However, on 18 occasions when neonates were found immediately after hatching but before having been fed, their mean weight was 3.19 (2.5-3.6) g, which was 79 percent of the weight of their eggs when fresh $(4.02 \ (3.5-4.9) \ g.)$. Wetherbee and Wetherbee (1961) reported an average egg weight of 3.98 (3.04-4.66) g for 14 clutches of redwing eggs and an average neonate weight of 2.75 (2.14-3.21) g for 12 clutches. Thus, neonates weighed 69 percent of the egg weights. Wetherbee and Wetherbee (1961) also reported on two other icterids: the Common Grackle (Quiscalus quiscula) (mean egg weight—6.76 g, mean neonate weight—4.96, 73 percent) and the Brown-headed Cowbird (Molothrus ater) (mean egg weight—3.03 g, mean neonate weight—2.22 g, 73 percent). Heinroth (1922) reported the weights of neonates as about two-thirds the weight of fresh eggs. When our calculations are combined with those of Wetherbee and Wetherbee (1961), the mean weight of neonates of redwing, common grackle, and cowbird are shown to be close to three-fourths of the egg weight.

Nice (1943) reported that neonate passerines weigh six to eight percent of the weight of their mother and that typically the young increase in weight 10- to 12-fold in the first 10 days of nest life. From our compilation, 18 adult female redwings had a mean weight of 41.6 g. If neonates have a mean weight of 3.19 g, they weigh 7.5 percent of mean adult weight. Fautin (1941) found that the most frequent weight for neonate Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) was 3.3 g and Ammann (1938) reported the mean adult female weight as 56.4 grams; thus, the neonates weighed about six percent of adult female weight. The weights of neonate cowbird (2.22 g) and common grackle (4.96 g) nestlings are 6.4 and 4.7 percent of adult weight, respectively. This percent is based on neonate weights given by Wetherbee and Wetherbee (1961) and on adult female weights for cowbirds (mean of two adults—38.55 g (Stewart, 1937), mean of 15 immatures 33 g (Selander and Kuich, 1963), and mean of 10 adults—36.4 g (Meanley, 1964). A weight of 93.0 g for an adult female grackle was given by Meanley (1964) and the mean weight of 26 females taken by Holcomb at Johnstown, Ohio, in January, 1967, was 106.6 g.

Weights and Measurements of Redwing Nestlings Compared to Adult Sizes Throughout the Nestling Period

Male and female redwing nestlings increased their weight 10-fold and 7.5-fold, respectively, in the first 10 days of nest life and weighed 54 and 67 percent of adult weight, respectively (table 2). The daily percent of increase in weight over the previous day was greater in males, but, since adult females are smaller than males, the females had attained a higher percent of the adult weight by day 10. Fautin (1941) reported that Yellow-headed Blackbird nestlings leave the nest at about 10 days, and that, at that time, the average weight of males is 54 grams and the average weight of females is 36 grams. This amounts to 59 percent and 64 percent of the adult weights, respectively. Nice (1943) reported that most passerines had reached 60 to 80 percent of adult weight by 10 days. The redwing males had gained only 54 percent of adult weight by ten days, but females had gained 67 percent. It may be that the overall development of nestlings in redwings (especially males) is slower than in many other passerines, as suggested by Wetherbee (1961). Immature redwing females had attained full adult weight by their first autumn; males had not.

The greatest daily increases in total length of nestlings occurred on days 2 through 6. Female and male nestlings reached 50 percent of adult length on days 8 and 10 respectively (table 3). The mean and percent increase in tarsus length each day for males and females is shown in table 3. Greatest mean increases in length came between days 1 and 7. The percent in gain over the previous days

redwing nestlings compared with adult size									
	Sex	Ν	Mean Weight	Percent Immature Wt.	Percent Adult Wt.	N	Mean Length (mm)	Percent Adult Length	
Day	М	47	3.9	7	6				
Õ	\mathbf{F}	58	3.8		9				
Day	Μ	42	6.1	10	9 9				
ĩ	\mathbf{F}	62	6.0		14				
Day	Μ	42	9.5	16	13	28	1.0	1	
$\tilde{2}$	\mathbf{F}	60	9.0		21	35	1.0	1.5	
Day	Μ	44	13.4	22	19	28	3.0	4	
3	\mathbf{F}	61	12.7		29	32	4.0	6	
Day	Μ	43	18.9	32	27	26	8.0	10	
4	F	54	16.6		38	33	9.5	14	
Day	М	42	24.2	40	34	30	14.5	18	
5	\mathbf{F}	59	21.1		49	36	16.0	24	
Day	Μ	46	28.4	47	40	27	22.0	27	
6	\mathbf{F}	61	24.3		56	34	23.5	35	
Day	Μ	45	32.5	54	46	24	28.0	34	
Day 7	\mathbf{F}	64	26.1		60	33	29.5	44	
Day	Μ	41	34.9	58	50	20	34.5	42	
8	\mathbf{F}	55	27.3		63	28	35.0	52	
Day	Μ	34	37.7	63	53	16	40.0	49	
ğ	\mathbf{F}	41	28.5		66	23	40.5	60	
Day	Μ	23	38.4	64	54	12	44.5	55	
10	F	18	28.9		67	13	43.5	65	

TABLE 2

Mean weight (grams) and first primary length (mm) of male and female reducing nestlings compared with adult size

TABLE 3

Mean total length, tarsus length, wing length, and lower manidbular tomium length in male and female redwing nestlings compared with adult size

	Sex	N	Mean Total Length (mm)	Percent Adult Length	Mean Tarsus Length (mm)	Percent Adult Length	Mean Wing Length (mm)	Percent Adult Length	Mean Tomium Length (mm)	Percent Adult Length
Day	M	34	$\begin{array}{r} 48.0 \\ 47.0 \\ 52.5 \end{array}$	21	$7.3 \\ 7.3 \\ 8.9 \\ 9.1 \\ 11.4$	25	8.5 8.5 10.0 10.5	7	7.5	33
Day 0	\mathbf{F}	36	47.0	24	7.3	28	8.5	8	8.0	40
Day	M F M	36 29	52.5	$\begin{array}{c} 21\\ 24\\ 23\\ 27\\ 27\\ 30\\ 30\\ 34\\ 34\\ 39\\ 38\\ 43\\ 41\\ 45\\ 44\\ 48\end{array}$	8.9	31	10.0	7 8 10 11 13	8.0 9.5 9.5 11.0	42
Day 1	F M	37	$52.5 \\ 53.5 \\ 62.5 \\ 60.5 \\ 69.5 \\ 68.5 \\ 79.5 $	27	9.1	34	10.5	10	9.5	47
${f Day \ 2}$	Μ	30 38	62.5	27	11.4	39	$\begin{array}{c}13.0\\13.5\end{array}$	11	11.0	48
2	FMFMFM FMFM FMF FMF	38	60.5	30	$11.4 \\ 14.4 \\ 14.6$	43	13.5	13	$ \begin{array}{r} 11.0 \\ 12.5 \\ 12.5 \\ 13.5 \\ 13.5 \\ \end{array} $	54
Day 3	Μ	31	69.5	30	14.4	50	17.5	$14 \\ 18 \\ 21 \\ 25 \\ 27 \\ 33 \\ 34 \\ 39 \\ 38 \\ 45 \\ 43 \\ 49 \\ 47 \\ 47 \\$	12.5	$\overline{55}$
3	F	36 29	68.5	34	14.6	$\begin{array}{c} 55 \\ 62 \end{array}$	18.5	18	12.5	62
Day 4 Day 5	M	29	79.5	34	17.9	62	25.0	21	13.5	59 67
_ 4	F	33	77.5	39	17.8	67	25.0	25	13.5	67
Day	M	$32 \\ 36$	$\begin{array}{c} 88.0\\ 84.5\end{array}$	38	$21.0 \\ 20.8 \\ 23.6 \\ 23.3 \\ $	$\overline{72}$	$\begin{array}{c} 33.0\\ 33.0\end{array}$	27	14.5	64
5	F	36	84.5	43	20.8	79	33.0	33	$\begin{array}{c}14.5\\15.5\end{array}$	72
Day 6	M	34	94.5	41	23.6	81	41.0	34	15.5	$\begin{array}{c} 68 \\ 72 \end{array}$
- 6	F	$ 34 \\ 36 \\ 32 $	90.0	45	23.3	88	39.5	39	14.5	72
Day 7	IVI D	32	101.0	44	26.1	90	46.5	38	16.0	70
D	F M	39 28	96.0	48	24.6	93	45.0	40	15.0	74 73
Day 8		28 38	105.5	40	21.4	$\begin{array}{c} 94 \\ 97 \end{array}$	52.0	43	16.5	13
Davi	Г	38 23	102.0	46 51 48	$27.4 \\ 25.6 \\ 28.0 \\ 26.2 \\ 29.0 \\ 0$	97 97	$\begin{array}{r} 49.5\\ 56.5\end{array}$	49	$15.5 \\ 16.5 \\ 15.5 \\ 17.0 $	77 73
Day 9	IVI F	$\frac{23}{29}$	$112.0 \\ 107.5$	$\frac{48}{54}$	20.0 26 2	97 99	50.5 53.0	47	10.0	73 77
Dov	Г	18	107.5 116.5	50	20.2	99 100	61.5	00 51	15.5	75
Day 10	М F	17	110.0	50	$29.0 \\ 26.3$	100	56.0	56	16.0	70
10	Г М		111.5	50 56 53	20.0	100	0.00	53 51 56 53	16.0	$\frac{79}{22}$
Day 11	${f M} {f F} {f M}$	7	122.5	53	29.3		64.0	53	17.5	77
Der	F M	$\frac{1}{2}$	$115.0 \\ 126.5$	==	26.0		55.0		16.0	
Day 12	1V1		120.0	55	29.5		67.0	55	17.5	77

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remained about the same for males and females until day 7. Fifty percent of adult tarsus length was attained by day 3 in both sexes. It is of particular importance to note that 100 percent of adult tarsus length was attained by day 10 in both sexes. The tarsus serves as a body support (Holcomb, 1966) and is a functional part of movement and locomotion before any of the other characteristics studied. Therefore, one might expect it to be developed to a greater extent than the wing chord (table 3). Williams (1940) found a mean of 25.68 mm and 29.15 mm for mean tarsal length on day 10 in female and male redwings, respectively. These values are very similar to those (26.3 and 29.0) reported here.

Greatest increases in mean wing length were on days 4, 5, and 6. Females and males had attained 50 percent of adult wing length by day 8 and 10, respectively. This may have an important bearing on the time that each sex leaves the nest and perhaps influences the ultimate sex ratio discussed by Holcomb and Twiest (In press).

The lower mandibular tomium increased rapidly in mean length over the initial 5 days of nest life and reached about 50 percent of adult size in both males and females by day 2 (Table 3). By day 10, males and females had obtained 75 and 79 percent of adult tomium length, respectively.

Mean increases in length of the first primary were greatest on days 5 and 6 (table 2), while mean weight increased most rapidly on days 4 and 5. Weight increases, however, declined rapidly after day 9, while the increase in primary length continued. Feathers were present on all tracts by day 6 and gained rapidly in length from then on (Holcomb and Twiest, In press).

DISCUSSION

Effect of Feather Growth on Weight Gain

Other observers have noted a decrease in rate-of-gain in weight as feathers were being produced or as temperature control was being established. Banks (1959) reported that the decrease in actual and relative gain in weight on the final three days of nestling life in the White-crowned Sparrow (Zonotrichia leucophrys) was probably due to a shift in the energy budget, as more food was utilized in production of feathers and heat. This same relationship has been suggested by Paynter (1954) for the Tree Swallow (Iridoprocne bicolor), and he also suggested it for the Barn Swallow (Hirundo rustica) from data presented by Stoner (1935). Kendeigh and Baldwin (1928) demonstrated the same concept for the House Wren (Troglodytes äedon), and Edson (1930) assumed there was a relationship between weight recession and feather development in the Violet-green Swallow (Tachycineta Lack and Silva (1948), in studies on the European Robin (Erithacus thalassina). rubecula), found that mean increase in weight dropped off sharply after day 7.5, when the primaries were splitting open. This would be the time when all feathers would be growing rapidly.

Putnam (1949) reported a rapid growth in weight of Cedar Waxwing (Bombycilla cedrorum) nestlings until the eighth and ninth days, with the most noticeable change in plumage on the ninth and tenth days. Mumford (1964) found the greatest mean weight gain on day 5 in the Acadian Flycatcher (Empidonax virescens), on which day all feather tracts had become visible. Similar relationships have been shown for the American Robin (Turdus migratorius) (Howell, 1942; Hamilton, 1935), Purple Martin (Progne subis) (Allen and Nice, 1952), Chipping Sparrow (Spizella passerina) (Weaver, 1937; Walkinshaw, 1944), Phoebe (Sayornis phoebe) (Stoner, 1939), Traill's Flycatcher (Empidonax traillii) (King, 1955), Henslow's Sparrow (Passerherbulus henslowii) (Hyde, 1939), Northern Cliff Swallow (Petrochelidon pyrrhonota) Stoner, 1945), Snow Bunting (Plectrophenax nivalis) and Lapland Longspur (Calcarius lapponicus) (Maher, 1964), American Goldfinch (Spinus tristis) (Walkinshaw, 1939), Tree Sparrow (Spizella arborea) (Baumgartner, 1938), Towhee (Pipilo erythropthalmus) (Barbour, 1950), Curvebilled Thrasher (*Toxostoma curvirostre*) (Rand, 1941), Long-billed Marsh Wren (*Telmatodytes palustris*) (Welter, 1935) and House Sparrow (*Passer domesticus*) (Weaver, 1942). However, Willson (1966) reported large increments in weight while feathers were developing in Yellow-headed Blackbird nestlings.

Differential Development Rate of Structures in Relation to their Function

Development of the different structures of nestlings was not uniform throughout the nestling period. Structures which were used most by nestlings while still in the nest developed more rapidly than structures which were not functional until the birds fledged. Therefore, we suggest that during the first 5–6 days, the main development is of those structures functional in life in the nest, while, during the last half of the nestling period, development occurs in those structures functioning in life after fledging.

The mouth is one of the first structures used by a young bird. The gape width, measured between commissural points, grew fastest between days 0 and 2. Between days 0 and 5, gape width increased by 5.7 mm, while during the second 5 days, it actually decreased by an average of 0.7 mm, due to a reduction in the fleshy rictal portions of the mouth.

The length of the lower ramus of the beak increased most rapidly between days 0 and 3. Between days 0 and 5, it increased 6.5 mm, but the increase was only 2 mm from days 5 through 10 (Holcomb and Twiest, In press).

A rough index of the size of the nestling's mouth can be obtained by multiplying gape width by length of beak (lower ramus), because the shape of the nestling's gaping mouth is roughly that of two triangles base to base. As applied to our data, this index increased from 76 on days 0 to 246 on day 6, after which it remained at 245 ± 5 until fledging. Between days 0 and 5, the index increased by 145, while only increasing by 19 between days 5 and 10.

The advantage of the above growth pattern is evident if the functions of the mouth are examined. In the nestling stage, young are fed by the adult placing food into that young bird's mouth which stretches highest and has the largest gape. An important use of the mouth and beak at this time is to provide a good target and feeding stimulus for the adult. After fledging, the young bird starts to forage, although still depending on the adult to supply some food. A pointed beak is best for adult foraging. During the entire nestling period, growth of the beak from nostril to tip was uniform. It increased 2.3 mm the first 5 days and 2.2 mm the second 5 days. The lower ramus also grew 2 mm during the last 5 days of the nestling period, the beak developed an adult shape, while maintaining the amount of surface area exposed in gaping. The mouth, therefore, maintained maximum functional capacity as a target for the parent, while developing into a structure which would have an entirely different function at maturity.

Legs are other rapidly developing structures. Tarsi grew fastest between days 2 and 5. During the first 5 days they grew 14 mm, but, during the second 5 days, they only grew 6.5 mm.

Feet, as measured by the span between toe one and three, also developed rapidly. The most rapid growth occurred between days 1 and 5. Between days 0 and 5 they gained 22 mm, but they grew only eight mm in the second 5 days.

Total length of the nestling, *excluding the caudal feathers*, increased most rapidly between days 2 and 5. In the first half of nestling life total length increased 39 mm, while only 17 mm were added in the last half.

The development of the feet, legs, and total length of a nestling all contribute to its ability to stretch for food. In addition, development of feet allows a nestling to grasp the bottom of the nest, thus reducing its chances of falling. The ability to grasp a branch and support its weight for a short time is not attained until day 7 or 8 (Holcomb, 1966). However, the ability to grasp the lining of the nest is developed a few days earlier (day 4 or 5). Grasping the lining of the nest with the feet does not require as much strength as does support of nestling weight. However, grasping does serve a purpose in preventing many nestlings from falling from the nest.

Brenner (1964) has shown that temperature control in the redwing develops throughout the nestling period. He further suggested that the nest and the brooding adult together produce a temperature adequate for development without a large expenditure of energy by nestlings. Therefore, there is less use for feathers during the nestling period than after the bird leaves the protection of the nest, when feathers become functional as insulation.

Feather development, excluding the primaries, during the first half of the nestling period was slight. During the second half, the feathers developed rapidly (days 0 to 5, 3.5 mm; days 5–10, 13.5 mm for the spinal tract).

The wing chord, including the eighth primary, developed rather uniformly throughout the entire nestling period. Approximately 25 mm were added each 5 days. However, rapid development did not start until day 3. Growth was then uniform until day 10. The primaries started development earlier than the rest of the contour feathers.

Flight is the chief function of the wing and primaries. By day 10, a nestling has attained approximately fifty percent of adult weight and wing length. This would be expected if the young bird is to be capable of some flight. The primaries started growing earlier than other feathers and attained a length adequate to permit some flight by day 10.

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