RELATIVE GROWTH, BODY CONSTITUENTS, AND ENERGY CONTENT OF NESTLING BARN SWALLOWS AND RED-WINGED BLACKBIRDS

ROBERT E. RICKLEFS

THE kinetics of growth include not only changes in gross weight, but also in the relative sizes of component parts (Brody, 1945; Laird, 1965) and in the relative proportions of the basic body constituents: water, protein, lipid, and ash (Bailey *et al.*, 1960). Changes in the constituents mean that the energy content per gram body weight also changes during the course of development.

In this study, body constituents and the weights of several body components in nestlings of two species of passerine birds, the Barn Swallow (*Hirundo rustica*) and the Red-winged Blackbird (*Agelaius phoeniceus*), were determined. Differential growth of body components and changes in the proportions of body constituents are presented, and energy contents are calculated from these data.

MATERIALS AND METHODS

In May and June, 1965, 41 nestling Barn Swallows and 22 nestling Red-winged Blackbirds were collected in the vicinity of Philadelphia, Pennsylvania. The young of each brood were usually removed over a period of several days to avoid possible undernourishment as the nestlings grew. All of the nestlings were collected during the middle of the day and were frozen for later analysis. When unknown, ages were estimated by comparing linear measurements with data from Stoner (1935) for the Barn Swallow and from my own measurements for the Red-winged Blackbird.

Barn Swallow nestlings normally fledge when they are 18 to 21 days of age and have attained adult weight. Red-winged Blackbirds leave the nest between 9 and 12 days and have attained approximately two-thirds of adult weight at that time. Blackbirds also exhibit sexual dimorphism in growth, males being about a third again as heavy as females at 9 days (Williams, 1940; Celia Haigh, pers. comm.). In this study, nestlings were not sexed and are treated together. While this produces considerable variation in absolute weights, little spread appears in the various weight-specific indices used in the analysis.

Before being processed, the blackbirds were dissected into the following parts: integument (skin and feathers), head, wings, legs, pectoral muscles, heart, liver, stomach, and the remainder of the body. Care was taken to remove fat deposited externally to the pectoral muscles, heart, and stomach, so this would be included with the body component. Of the swallows, 33 were analyzed whole (with the stomach contents removed) and the remaining 8, ages 9 to 19 days, were dissected into integument, pectoral muscles, heart, liver, stomach, and the remainder of the body including wings, legs, and head.

The components were weighed on an analytical balance and then dried in a vacuum desiccator at 50–55° C for at least three days. The difference in weight before and after drying (*wet weight* minus *dry weight*) is the *water content*. The dried components were extracted in a 5 : 1 mixture of petroleum ether (30–60° C) and chloroform (C. W. Helms, pers. comm.) for four days, fresh solvent being

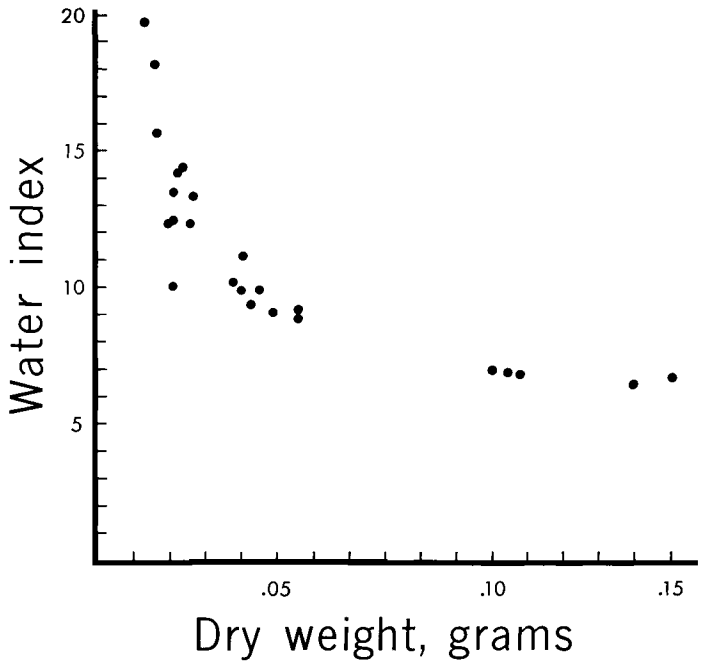

Figure 1. Changes in the water index (based on dry rather than lean dry weight) of Barn Swallow embryos as a function of size.

substituted at least once, then vacuum dried for three to four hours and weighed. The difference between the weights before and after extraction (*dry weight* minus *lean dry weight*) is the *lipid content*. The extracted components were then combusted in a muffle furnace at 500–550° C to determine *ash content*.

Water content and dry weight were determined for a series of 24 Barn Swallow embryos from eggs collected in the same vicinity as the nestlings. These were not aged.

RESULTS

Relative growth.—With the exception of the stomach and the liver, the components of nestling Red-winged Blackbirds are related exponentially to the total body weight throughout the nestling period (0–12 days) by the formula

$$W_c = aW_t{}^b$$

where W_c is the weight of the component, W_t is the total weight of the nestling, and a and b are constants. Values of the exponent b which are greater than 1.0 indicate that the component is increasing in weight faster than the nestling as a whole and thus is becoming relatively larger. Similarly, values of b which are less than 1.0 indicate that the relative growth

TABLE 1

RELATIVE POST-NATAL GROWTH CONSTANTS OF BODY COMPONENTS OF RED-WINGED BLACKBIRDS, PIGEONS, AND CHICKENS[1]

Component	*Red-winged Blackbird*		*Pigeon*[2]	*Chicken*[3]
	Lean dry weight	*Wet weight*		
Head	0.72	0.67	0.54 (brain)	0.22 (brain)
Body	0.79	0.89		
Legs	1.22	1.21		
Wings	1.34	1.36		1.14
Pectoral muscles	1.69 (3–12 days)	1.92 (3–12 days)		(muscular system)
Integument	1.37	1.34		1.00 (skin only)
Liver	1.69 (0–5 days)[1]	1.64 (0–3 days)	1.6 (1–3 days)	0.44, 0.67
	0.79 (5–12 days)	0.94 (3–12 days)	1.1 (3–9 days)	
			0.4 (9–21 days)	
Stomach	1.18 (0–5 days)	1.19 (0–3 days)		0.30
	0.36 (5–12 days)	0.22 (3–12 days)		0.48 (gizzard)
Heart	0.98	1.02	1.80 (0–3 days)	0.20
			1.04 (3–9 days)	
			0.75 (9+ days)	

[1] In instances where the growth rate changes continuously, the average rate of change is given for two or more periods. The periods represented are arbitrary, i.e., they do not represent meaningful phases of growth.

[2] From Brody (1945).

[3] From Brody (1945) and Latimer (1924).

rate of the component is slow and thus it is becoming smaller in relation to the total weight of the nestling.

Relative growth constants (b) are presented for the components of the Red-winged Blackbird in Table 1 with comparative data for the pigeon (*Columba livia*) and the chicken (*Gallus domesticus*) (Brody, 1945). In the blackbird, high relative growth rates characterize locomotory and insulative components (legs, wings, pectoral muscles, integument) and, during the early stages of nestling growth, the liver and stomach. The relative weight of the heart to the whole body does not change during the nestling period. The body component (which includes the intestines), the head, and, during most of the period of nestling growth, the stomach and liver decrease in relative size. The functions of these components in altricial nestlings are primarily food receiving and processing.

Water content.—For comparative purposes, the amount of water in

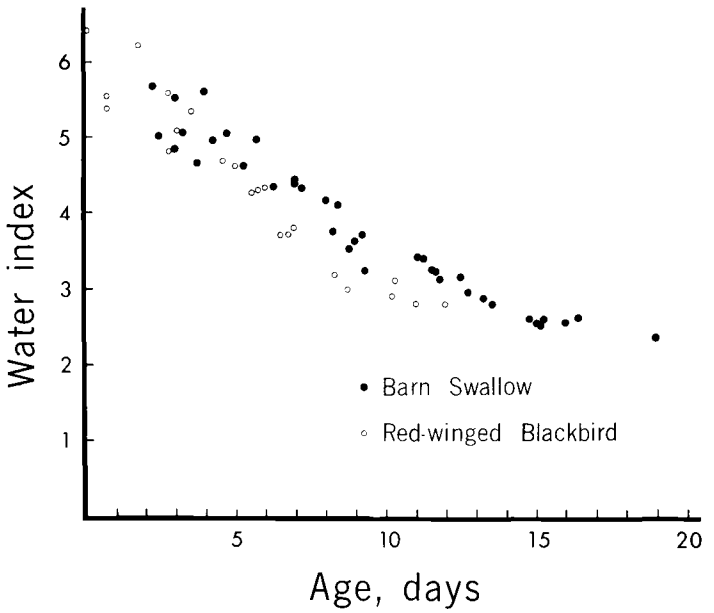

Figure 2. Changes in the water index of nestling Barn Swallows and Red-winged Blackbirds as a function of age.

the various components is expressed as the *water index* (the water content divided by the lean dry weight). Because of evaporation during dissection the water index is often somewhat lower than the actual value, especially in the smaller specimens and components. In no case was the loss of water during dissection more than 5 per cent of the original weight of the bird.

A general decline in the water content of the tissues occurs during the embryonic period (Figure 1) and persists through fledging (Figures 2 and 3). The water index of the head was the highest for the components analyzed, and the integument becomes the driest at the time when the feathers elongate and dry out. The patterns of water loss in the heart, liver, and stomach are similar to each other. As a group they differ from the pectoral muscles, legs, and wings, whose indices are higher at hatching but decrease to a level which is similar to the heart, liver, and stomach by the time of fledging. The decrease in the relative water content persists in the older swallow nestlings (9–19 days), especially in the integument, but also in the body, pectoral muscles, liver, and heart (Table 2). The water index of the stomach shows little change during this period.

The relative water content of blackbirds at fledging (about 2.8) is

TABLE 2
WATER INDICES OF BODY COMPONENTS OF NESTLING BARN SWALLOWS

Individual	*Age (days)*	*Head and body*	*Skin and feathers*	*Pectoral muscles*	*Liver*	*Stomach*	*Heart*
G2	9.2	4.1	3.0	4.1	3.6	3.0	4.1
E4	11.1	3.8	2.7	3.8	3.7	3.0	4.3
I2	11.6	3.7	2.2	3.5	3.6	3.1	3.9
C3	11.6	3.7	2.1	3.7	3.0	3.2	3.7
C4	12.7	3.5	2.0	3.5	3.0	3.4	3.4
I4	15.1	3.2	1.3	3.2	3.1	3.2	3.5
G5	15.3	3.3	1.3	3.2	3.2	2.9	3.5
K4	18.9	3.0	0.9	3.0	2.7	3.3	3.4

higher than that of adults. For comparison, average water indices calculated for 2 adult male and 10 adult female Red-winged Blackbirds are 2.1 and 2.0, respectively (data from E. P. Odum, pers. comm.). Similar data are not available for adult Barn Swallows but the water indices of fledglings (about 2.3) are more nearly comparable with adults of other passerine species. Kale (1965) determined the water index to be 2.6 in adult Long-billed Marsh Wrens (*Telmatodytes palustris*). Values of 2.3 can be calculated from data given for both the Myrtle Warbler, *Dendroica*

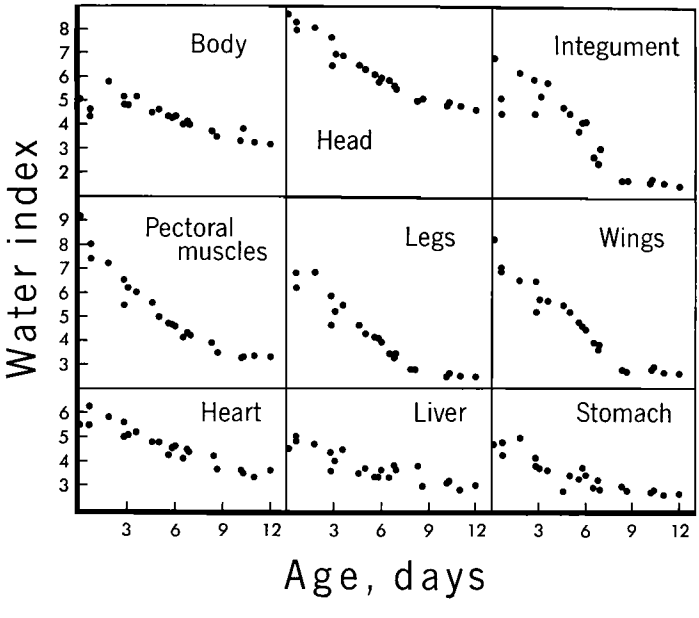

Figure 3. Changes in the water indices of components of nestling Red-winged Blackbirds as a function of age.

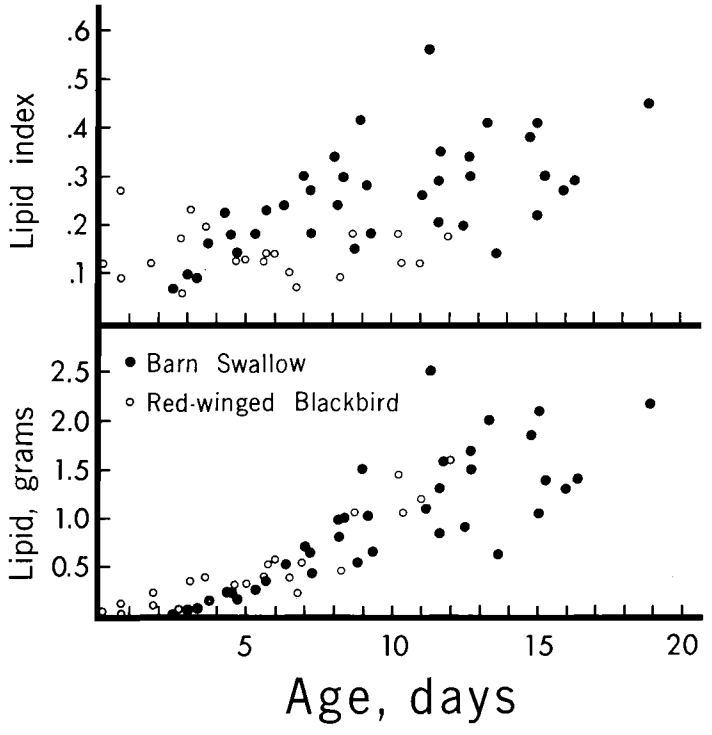

Figure 4. Total lipid content (below) and lipid indices (above) of nestling Barn Swallows and Red-winged Blackbirds as a function of age.

coronata (Yarbrough and Johnston, 1965), and the Dickcissel, *Spiza americana* (Zimmerman, 1965). The average relative water content of adult Slate-colored Juncos (*Junco hyemalis*) is 2.2 (Farrar, 1966).

Lipid deposition.—The *lipid index* used in this analysis is the lipid content divided by the lean dry weight. Total lipid content and lipid indices of the Red-winged Blackbird and Barn Swallow nestlings are presented in Figure 4. Relative lipid levels were generally higher in the swallow than in the blackbird except for the first three or four days when the reverse was true. Lipid indices for the components of the blackbird and swallow nestlings are summarized in Table 3. No clear trends were observed in the lipid levels of individual components of blackbird nestlings 0–12 days of age or of swallow nestlings 9–19 days of age. The higher values for the body and integument result from the visible, subcutaneous fat deposits. One high value (0.46) obtained for the body component of a nestling blackbird less than one day old was apparently due to the presence of yolk in the intestine.

TABLE 3
AVERAGE LIPID INDICES OF BODY COMPONENTS OF NESTLING BARN SWALLOWS AND RED-WINGED BLACKBIRDS

Component	*Red-winged Blackbird*[1]	*Barn Swallow*[2]
Head	0.10	0.46
Body	0.23	
Legs	0.06	
Wings	0.04	
Integument	0.17	0.19
Pectoral muscles	0.09	0.16
Liver	0.05	0.12
Stomach	0.03	0.12
Heart	0.08	0.17

[1] Based on 22 individuals, aged 0 to 12 days.

[2] Based on 8 individuals, aged 9 to 19 days.

Lipid indices of whole nestling swallows (0.15–0.55) are comparable to those of wintering Myrtle Warblers (0.21–0.68) but are not as high as pre-migratory levels in that species (up to 0.82; Yarbrough and Johnston, 1965). Zimmerman (1965) reported lipid indices of up to 1.50 in migrating Dickcissels, while winter levels ranged from 0.19 to 0.65. In White-throated Sparrows, *Zonotrichia albicollis* (Odum and Perkinson, 1951), pre-migration lipid indices averaged 0.67 and the lowest values, during molt and after migration, averaged 0.22. Winter levels in that species averaged 0.46. Lipid indices in summer Long-billed Marsh Wrens averaged about 0.45 (Kale, 1965).

TABLE 4
WEIGHT-SPECIFIC ENERGY CONTENTS OF SOME PASSERINES

Species and sample	*Lipid index*	*Energy content (kcals/g)*	*Source*
Red-winged Blackbird			E. P. Odum
Northern Florida, winter	0.34	2.17	(pers. comm.)
Long-billed Marsh Wren			Kale (1965)
Males	0.39	2.08	
Females	0.47	2.04	
Immatures	0.48	2.18	
Nestlings (0–5 days)		0.83	
Nestlings (5–9 days)		1.05	
Nestlings (9–13 days)		1.75	
Fledglings		1.87	
Myrtle Warbler			Yarbrough and Johnston (1965)
Least fat sample (coastal North Carolina, April)	0.21	1.57	
Fattest sample (Florida, January)	0.68	2.50	
Dickcissel			Zimmerman (1965)
Breeding males	0.12	1.38	
Migrating males	0.53	2.36	

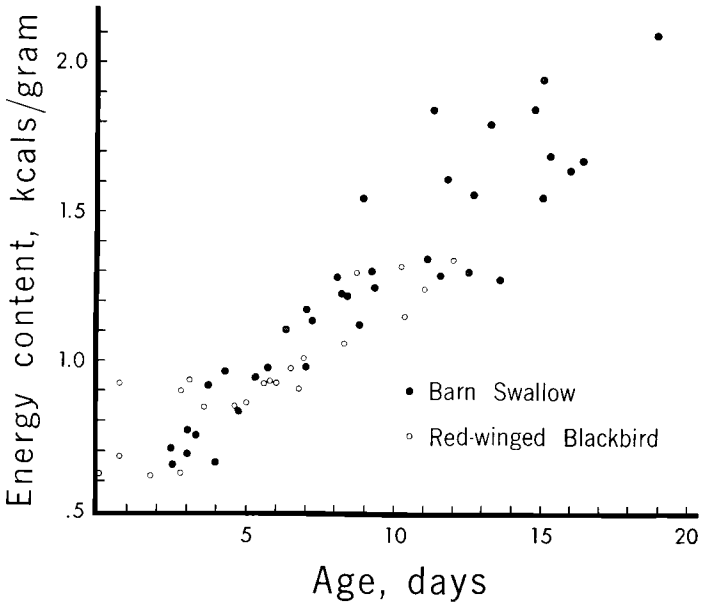

Figure 5. Changes in the weight-specific energy content of nestling Barn Swallows and Red-winged Blackbirds as a function of age.

Lipid indices of adult Red-winged Blackbirds (taken in Pennsylvania, in the summer) calculated from Brenner and Malin's (1965) data average 0.29. E. P. Odum (pers. comm.) has found lipid indices averaging 0.34 (range, 0.18–0.54) in 10 wintering (October to January) Red-winged Blackbirds in Florida. These values are nearly twice those found in nestlings aged at 5 to 12 days.

Ash content.—The *ash index* is the ash content expressed as per cent of the lean dry weight. Values for whole Barn Swallows vary between 8.5 and 10.5 per cent with a slight upward trend. The ash index of Red-winged Blackbird nestlings is high initially (13–15 per cent at hatching) and drops to about 10 per cent at five days of age before rising to about 12 per cent by the time of fledging. The percentage of ash in those components of the blackbird which do not contain skeletal structure (pectoral muscles, integument, heart, liver, and stomach) drops in the same manner as the water index, whereas in the wings, legs, and head the ash index rises rapidly, presumably with the deposition of mineral in the bones. The index increases from 9 to 23 per cent in the wings, 11 to 21 per cent in the legs, and from 12 to 18 per cent in the head. Decreases are greatest in the integument (10 to 3 per cent).

Energy content.—The total energy content, in kcals, of the nestling

can be calculated from data on the lipid content and protein content (roughly lean dry weight minus ash) using the thermal equivalents given by King and Farner (1961: 219): one gram of protein and one gram of lipid are equal to 4.2 kcals and 9.5 kcals of metabolizable (excretory losses not included) energy, respectively. Values for the weight-specific energy content (kcals/gram wet weight) of nestling Barn Swallows and Red-winged Blackbirds are presented in Figure 5. In both species this index increases markedly during development, as a result of the decrease in water content and, especially in the Barn Swallow, the deposition of lipid reserves. Comparative data for the young and adults of several other species have been calculated and are presented in Table 4.

I. L. Brisbin (pers. comm.) has found that in two species with precocial chicks, the Herring Gull (*Larus argentatus*) and randomly bred domestic chickens, weight-specific energy content is high in the newly hatched young, about 2.2 and 1.6 kcals per gram, respectively, and does not increase as the chick grows. These values are more than twice those found at an early age for the altricial nestlings in this study. The discrepancy results primarily from the higher lipid levels of the precocial chicks, but also reflects a reduced water index (4.8 and 4.9 at hatching in the gull and chicken, respectively).

DISCUSSION

Concomitant with the changes in water content, weight-specific energy, and relative sizes of body components, which have been examined in this study, growth in birds is also accompanied by changes in weight-specific metabolic rates (Dawson and Evans, 1957) and a persistent decline in the over-all relative growth rate (Dawson and Evans, 1960; Kahl, 1962; Maher, 1964). Although this study was designed to be solely descriptive, it is clear that the type of analyses employed here will be useful in studies of the energetics and dynamics of growth. The growing organism can form a limited quantity of tissue which must be allocated to the various organs such that the over-all body organization is most efficient for its purpose. An altricial nestling changes markedly during development from an organism designed for the most efficient conversion of energy into tissue, to one which must perform the maintenance activities of the adult. This shift is reflected in the anatomy and physiology of the nestling.

Several differences in developmental patterns are apparent between altricial and precocial young. The relative growth of the head, liver, and heart is much lower in precocial young although that of the stomach appears to be similar (see Table 1). Water indices at hatching in precocial chicks may be lower than in altricial young, possibly reflecting

the more mature state of tissues in the former. Immediate energy reserves in the newly hatched chick, which are higher in precocial species, appear to be correlated with these birds' developmental maturity and activity. The lipid stores present in precocial chicks at hatching may provide insurance in case the chick does not learn how to obtain food quickly after hatching, or in case weather conditions are adverse. This latter must affect precocial young to a greater extent than altricial young which are protected by the nest and parental brooding.

Patterns of energy storage in nestlings must reflect certain aspects of breeding ecology. It is not known whether lipid deposition in nestlings acts as insurance against fluctuations in feeding conditions, or whether changes in lipid levels occur after fledging when energy demands of species such as swallows must greatly increase. The low levels of lipid reserves in nestling Red-winged Blackbirds are puzzling in view of the ever-present threat of starvation to marsh-nesting icterids (Orians, 1966; Willson, 1966).

ACKNOWLEDGMENTS

I would like to thank Dr. Carl Helms for advice on lipid extraction techniques, and Dr. Eugene P. Odum, Dr. Gordon Orians, I. Lehr Brisbin, and Celia Haigh for reading an early version of the manuscript and offering many helpful suggestions and pertinent information. This work was supported by a National Science Foundation Graduate Fellowship.

SUMMARY

The differential growth rates of body components in 41 nestling Barn Swallows and 22 nestling Red-winged Blackbirds were studied. The locomotory organs and integument (plumage) become progressively larger, while food processing organs and the head decline in relative size.

The water index of the tissues declines, as the nestling develops, from approximately 6 at hatching to between 2 and 3 at fledging. All of the body components studied (heart, liver, stomach, pectoral muscles, limbs, head, integument) exhibit this decline to a greater or lesser extent.

The lipid content of both species increases with age, but lipid indices reached much higher levels, comparable to adults, in the swallow nestlings.

Ash content, expressed as a percentage of the lean dry weight, does not change appreciably in the nestling as a whole, but increases in those components which contain bone and decreases in the soft organs.

The weight-specific energy content of nestlings (kcals per gram of wet weight) was calculated from data on body constituents and their thermal equivalents. This index increases from approximately 0.6 at hatching to about 1.3 and 2.0 at fledging in the blackbird and the swallow, respectively.

LITERATURE CITED

BAILEY, C. B., W. D. KITTS, AND A. J. WOOD. 1960. Changes in the gross chemical composition of the mouse during growth in relation to the assessment of physiological age. Canadian J. Anim. Sci., **40**: 143–155.

BRENNER, F. J., AND W. F. MALIN. 1965. Metabolism and survival time of the Red-winged Blackbird. Wilson Bull., **77**: 282–289.

BRODY, S. 1945. Bioenergetics and growth. New York, Reinhold.

DAWSON, W. R., AND F. C. EVANS. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. Physiol. Zool., **30**: 315–327.

DAWSON, W. R., AND F. C. EVANS. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor, **62**: 329–340.

FARRAR, R. B., JR. 1966. Lean dry weight and water balance in Slate-colored Juncos. Auk, **83**: 616–622.

KAHL, M. P., JR. 1962. Bioenergetics of growth in nestling Wood Storks. Condor, **64**: 169–183.

KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren in Georgia salt marshes. Publs. Nuttall Orn. Club, No. 5.

KING, J. R., AND D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215–288 *in* Biology and comparative physiology of birds (A. J. Marshall, ed.). New York, Academic Press.

LAIRD, A. K. 1965. Dynamics of relative growth. Growth, **29**: 249–263.

LATIMER, H. B. 1924. Postnatal growth of the body, systems and organs of the single-comb white leghorn chicken. J. Agric. Res., **29**: 363–399.

MAHER, W. J. 1964. Growth rate and development of endothermy in the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*) at Barrow, Alaska. Ecol., **45**: 520–528.

ODUM, E. P., AND J. D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., **24**: 216–230.

ORIANS, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor, **68**: 321–337.

STONER, D. 1935. Studies on the Barn Swallow. Auk, **52**: 216–230.

WILLIAMS, J. F. 1940. The sex ratio in nestling eastern Red-wings. Wilson Bull., **52**: 267–277.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr., **36**: 51–77.

YARBROUGH, C. G., AND D. W. JOHNSTON. 1965. Lipid deposition in wintering and premigratory Myrtle Warblers. Wilson Bull., **77**: 175–191.

ZIMMERMAN, J. L. 1965. Carcass analysis of wild and thermal stressed Dickcissels. Wilson Bull., **77**: 55–70.

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania. Present address: *Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Canal Zone.*