GROWTH AND DEVELOPMENT OF THE RUFOUS-WINGED SPARROW (*AIMOPHILA CARPALIS*)

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Growth and development of birds have engendered considerable recent interest. Rate of increase in body weight is known for many species (Ricklefs 1968a, 1972), but development of homeothermy (e.g., Kendeigh 1939, Dawson and Evans 1957, 1960, Ricklefs and Hainsworth 1968), relative growth of organs and changes in body composition (Ricklefs 1967a, 1975, Myrcha and Pinowski 1969, Diehl et al. 1972) are poorly known. Few attempts have been made to correlate all these factors in one species (Diehl et al. 1972, Diehl and Myrcha 1973, Ricklefs 1975). Herein, we compare growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*), which has a short nestling period (8–9 days), to those of the Cactus Wren (*Campylorhynchus brunneicapillus*), with a nestling period of 20 days (described in detail by Ricklefs and Hainsworth 1968 and Ricklefs 1975).

METHODS

The Rufous-winged Sparrow is a locally common resident of shrubby grasslands in southern Arizona and Sonora, Mexico. Its life history has been described by Ohmart (1969). Growth, development of homeothermy, and behavioral changes in nestlings of known age were studied during July, August and September, 1970 and 1971, on the Santa Rita Experimental Range, Pima County, Arizona. Young were weighed and measured between 05:00 and 09:00. We measured the bill (from nares), wing (flesh only), wing chord, length (exposed) of third primary, tarsus, length (exposed) of second rectrix, and width of flange. Sequence of feather eruption, age at eye opening, and changes in behavior were noted.

To study development of homeothermy, we removed nestlings from their nests and took their body temperature (T_b, proventricular) with a Schultheis quick-registering thermometer. We then placed them in a portable ice chest containing two half-gallon containers of ice for 40–45 min. Air temperature in the ice chest could be maintained below 25°C and remained relatively constant (± 1°C in 11 trials, checking temperatures at 5-min intervals). Birds were insulated from direct contact with the ice by at least 2 cm of newspaper. Body temperature was taken immediately on removal of the bird from the chamber, and the nestlings were returned to their nest.

Fourteen nestlings of known age, five juveniles, and three adults were collected in the same general area for analysis of constituents and organ weights following the methods described in Ricklefs (1967a, 1975). Wet weight minus dry weight is the water content; dry weight minus lean dry weight is the lipid content. Wing areas were obtained by tracing the outline of the extended wing onto paper and weighing the outlined portion. Wing loading, expressed as g/cm², was calculated as body weight divided by the area of both wings.

An ash index was calculated for Rufous-winged Sparrows as the ash weight of head, body, legs and wings divided by total lean dry weight. Components not containing bone were not ashed for all specimens. The approximate mineral content of the skeleton was calculated by subtracting the estimated amount of dissolved salts in the tissues from the total ash content. The dissolved salts were estimated from the average salt content per gram of water in tissues not containing bone (liver, pectoral muscle and stomach: 0.024 g ash/g water). Ash content of bone was then calculated by the expression: bone ash = total ash − 0.024 water.

Energy content of the sparrows was calculated utilizing energetic equivalents of 9.0 kcal/g lipid and 5.5 kcal/g ash-free lean dry weight.

GENERAL DEVELOPMENT AND GROWTH

At hatching, a Rufous-winged Sparrow was naked except for patches of dark gray down. On day 1, most primaries and, in some birds, the distal secondaries appeared above the surface of the skin. With the growth of the primaries during the first day, the width of the manus more than doubled. On day 2 all primaries, secondaries, alular remiges, greater secondary coverts, proximal greater primary coverts and some ventral and dorsal body feathers appeared. Nearly all feathers except the rectrices and head feathers appeared by the end of day 3. Rectrices appeared by day 4 and most head feathers by day 5.

Primaries, secondaries, alular quills and a few dorsal and ventral body feathers started to emerge from their sheaths on day 5. Most other feathers followed by day 6, but rectrices had not emerged from their sheaths until day 7, and some anterior head feathers were still completely ensheathed at 9 days. The approximate sequence of feather development is presented in table 1.

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TABLE 1. Sequence of feather development in the Rufous-winged Sparrow.

Age (days)[a]	Appear above skin (sequence)	Age when feathers begin to emerge from sheaths (sequence)	
1	Primary remiges (nearly simultaneously)	5	(proximal to distal)
	Secondary remiges (distal to proximal)	5	(distal to proximal)
2	Secondary coverts (distal to proximal)	6	(distal to proximal)
	Alular remiges (distal to proximal)	5	
	Primary coverts (distal to proximal)	6	
	Humeral (posterior to anterior)	6	(posterior to anterior)
	Sternal	–	
	Axillar (dorsal to ventral)	5	
	Abdominal (anterior to posterior, central to lateral)	6	(central to lateral)
	Interscapular	6	(posterior to anterior)
	Femoral (posterior to anterior, ventral to dorsal)	6	(anterior to posterior)
	Spinal (posterior to anterior)	–	
3	Crural	–	
	Dorsal saddle (anterior to posterior)	6	(posterior to anterior)
	Sternal (anterior to posterior)	–	
	Middle secondary coverts	6	(distal to proximal)
	Middle primary coverts and alular coverts	–	
	Lesser coverts (distal to proximal)	–	
	Pelvic (anterior to posterior)	6	(posterior to anterior)
4	Head (except superciliaries, auricular, interramal, malar and frontal)	7–8	
	Rectrices (central to lateral)	7	
5	Rest of head	8–9	

[a] Day of hatching = 0.

The oral flanges were nearly pure white at hatching but took on a pale yellow color by day 3. The upper mandible was shorter than the lower until day 3. The egg tooth persisted through fledging. Eyes began to open by the end of day 2 and were fully open in most birds 5 days old. At hatching the abdomen was greatly distended but became less noticeable with the growth of the pectoral muscles.

At day 5, young Rufous-winged Sparrows could stand but not grasp. Six-day-old young grasped nesting material when they were removed from the nest. Seven-day-old nestlings often fledged when disturbed if nest mates were older; most young left the nest at eight to nine days of age, although one young remained until ten days.

Fledglings remained dependent on their parents for three or more weeks (minima of 21, 22, and 27 days after fledging for three broods). At first they remained hidden in grass; we located them only by their begging calls or by following adults carrying food. Later they were more active and followed the adults as they moved. Both adults cared for fledglings during the first few days; we do not know if one or both sexes were involved in later post-fledging care. In two first broods, dependency continued until at least two days after the hatching of eggs in a subsequent nest. Some independent foraging was noted for a fledgling 23 days old. At fledging, the young could flutter their wings but could not fly. They could, however, hop rapidly, and they quickly disappeared into the grass. Fledglings 12–17 days old flew weakly; flight characteristic of adults was noted in fledglings 24–38 days old. The maturation of flight by Rufous-winged Sparrows during the first week after fledging paralleled a rapid increase in wing area and decrease in wing loading (table 2). Eight individuals 14–19 days old had noticeably

TABLE 2. Surface area of wings and wing-loading of Rufous-winged Sparrows.

	Age (days)							At first molt	Adult
N	2 (1)	3 (1)	4 (2)	6 (2)	7 (1)	8 (4)	15 (2)	(1)	(2)
Surface area (cm^2)	2.7	4.8	13.1	21.1	23.9	36.2	69.9	81.7	84.3
Wing loading (g/cm^2)	1.83	1.36	0.60	0.49	0.46	0.34	0.20	0.20	0.18

short rectrices, and those of 7 fledglings 23–25 days old appeared fully grown. Nine individuals between ages 36 and 55 days were obviously molting, but three individuals 28–29 days old and three 37–38 days old showed no signs of molt. Two fledglings 41 days old were indistinguishable in the field from adults.

Growth data were obtained for 107 individuals, several of which were measured each day of the nestling period. Average weight on the day of hatching was 2.0 g (range 1.4–2.9); mean fresh egg weight was 2.0 g (table 3). When Rufous-winged Sparrows fledge, they weigh about 12 g, 78% of adult weight ($\bar{x}$ = 15.3 g, N = 34 adults in the University of Arizona collection).

The growth of the Rufous-winged Sparrow can be expressed by the logistic equation:

$$W = 12.3/1 + e^{-0.576(t-2.85)}$$

where W is weight, e is the base of the natural logarithms and t is age in days with day 0 as the day of hatching. The growth constant, $K = 0.576$, indicates rapid growth.

Of the body parts which we measured, only the tarsus reached adult size at fledging (table 4, fig. 1). The fleshy part of the wing (manus) attained nearly 90% of adult size at fledging, but neither the bill nor any feathers exceeded 70% of adult length, and the rectrices were less than 20% of adult length at fledging. Body parts continued to grow after fledging and approached adult size within seven weeks after hatching. The relative immaturity of the Rufous-winged Sparrow at fledging reflects the short nestling period.

TABLE 3. Increase in body weight (g) of Rufous-winged Sparrows.

Age (days)	N	Mean	SD	Range
Egg	13	2.0	0.14	1.7– 2.2
0	34	2.0	0.36	1.4– 2.9
1	47	3.3	0.51	2.7– 4.1
2	47	4.9	0.67	3.0– 6.1
3	46	6.5	0.79	4.5– 7.9
4	42	8.2	0.68	6.9– 9.7
5	32	9.7	0.72	8.4–11.0
6	29	10.6	0.78	9.1–11.6
7	31	11.2	0.79	9.7–13.3
8	21	12.1	0.68	10.8–13.5
9	5	11.9	0.36	11.4–12.3
12–18	6	13.6	0.59	12.5–14.3
First molt	3	15.5	0.79	14.6–16.1
Adult	34	15.3	0.97	13.3–17.4

BODY CONSTITUENTS

Water content of Rufous-winged Sparrows increased steadily during the growth period and leveled off after fledging to about adult values (fig. 2). A slight increase above this level, noted for birds in their first molt, was caused by the high water content of the growing feathers. The water index (water

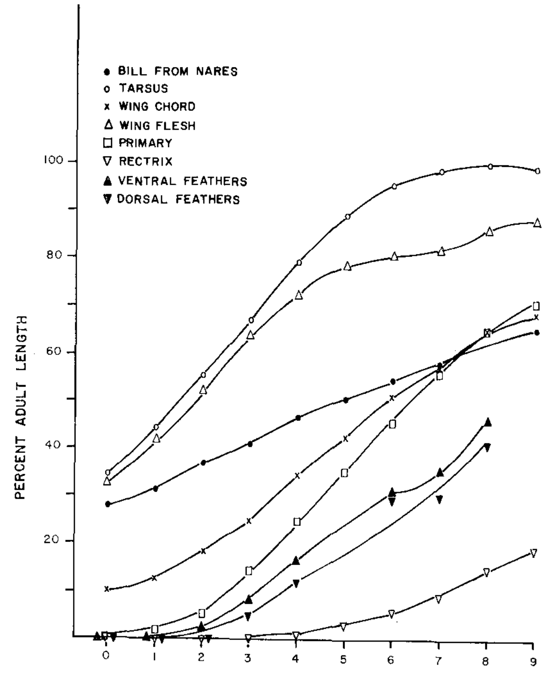

FIGURE 1. Linear growth of Rufous-winged Sparrows in relation to adult size.

TABLE 4. Measurements (mm) of Rufous-winged Sparrows.[a]

Age	Bill	Wing flesh	Wing chord	Primary	Tarsus	Rectrix	Flange
0	2.0	6.1	6.1	0	6.5	0	7.7
	0.26	0.59	0.59	–	0.77	–	0.54
	1.5–3.1	4.6– 7.5	4.6– 7.5	–	4.3– 8.0	–	6.5– 8.8
1	2.3	7.7	7.7	0.5	8.4	0	9.0
	0.20	0.83	0.87	0.46	0.94	–	0.51
	2.0–2.7	6.1–10.1	6.1–10.1	0 – 2.0	6.2–10.6	–	7.9–10.0
2	2.7	9.8	10.7	2.6	10.6	0	10.0
	0.20	0.94	1.40	1.01	0.98	–	0.59
	2.2–3.2	7.4–11.3	7.4–13.1	0.5– 4.8	8.7–12.8	–	8.9–12.1
3	3.0	12.1	15.1	6.6	12.7	0.02	10.5
	0.23	0.97	2.00	1.91	1.18	0.10	0.36
	2.3–3.7	9.9–13.8	10.9–18.7	2.1–11.2	10.5–15.0	0 – 0.6	9.9–11.6
4	3.4	13.7	20.8	11.7	15.1	0.5	10.7
	0.20	0.65	1.90	1.99	0.90	0.40	0.34
	3.0–4.0	12.1–15.2	15.6–24.1	6.8–16.2	13.1–17.6	0 – 1.6	9.9–11.4
5	3.7	14.8	25.6	16.7	17.0	1.9	10.7
	0.26	0.66	2.16	1.98	0.87	0.50	0.44
	3.2–4.5	13.3–16.1	20.5–30.0	11.5–21.8	15.1–18.6	1.0– 2.9	9.8–11.5
6	4.0	15.2	30.8	21.6	18.1	3.7	10.6
	0.27	0.67	1.77	1.61	0.63	1.10	0.38
	3.4–4.7	13.5–16.3	26.4–33.7	18.0–25.6	17.0–19.6	2.1– 6.4	9.9–11.2
7	4.3	15.5	35.1	26.7	18.8	5.9	10.3
	0.30	0.99	2.00	2.92	0.75	2.00	0.36
	3.9–5.0	12.6–17.5	29.3–38.2	21.1–36.4	17.0–20.3	2.9–10.1	9.6–11.2
8	4.6	16.2	39.8	31.0	19.1	9.3	10.3
	0.27	0.50	1.58	3.20	0.73	1.75	0.39
	4.1–5.2	15.0–17.2	37.1–42.7	21.8–38.1	18.1–20.3	6.2–12.4	9.8–11.4
9	4.8	16.5	41.4	33.1	18.8	11.8	10.3
	0.24	0.40	1.48	1.72	0.32	1.78	0.38
	4.5–5.1	15.9–16.8	39.8–43.1	31.0–35.4	18.4–19.2	8.9–13.4	9.7–10.7
Adult	7.3[b]	18.8[c]	60.9[b]	47.2[c]	19.0[b]	63.6[b]	–
	0.19	1.30	1.71	3.47	0.42	1.96	–
	7.1–7.6	16.8–21.2	58.2–64.3	42.2–51.1	18.4–19.9	59.2–65.5	–

[a] N as in table 3, except where noted; values given are mean (above), standard deviation (middle), and range (below).
[b] N = 12.
[c] N = 8.

content divided by lean dry weight) decreased rapidly to about 2.7 at fledging, considerably above the adult level of 1.9 (fig. 3).

The lean dry constituent increased rapidly during the nestling period and more slowly post-fledging (fig. 2). Adult lean dry weight was not reached by the time of the first molt (30–60 days after fledging). The lipid content of nestlings was low (fig. 2). The fat index (fat weight divided by lean dry weight) varied between 0.1 and 0.2 during the nestling period and was greatest just before fledging

TABLE 5. Ash content of skeletal components of Rufous-winged Sparrows.

Age (days)	No. of birds	Ash content of bone (g)[a] body	head	legs	wings	total
8	4	0.045	0.017[b]	0.054	0.031	0.152[b]
		(0.005)	(0.003)	(0.004)	(0.005)	(0.018)
13–15	2	0.075	0.034	0.062	0.050[c]	0.203[c]
		(0.019)	(0.002)	(0.007)	(—)	(—)
Juvenile	2	0.088	0.051	0.071	0.057	0.266
		(0.004)	(0.001)	(0.001)	(0.005)	(0.004)
Adult	3	0.110	0.114	0.086	0.082	0.391
		(0.005)	(0.004)	(0.007)	(0.011)	(0.026)

[a] Mean and standard deviation (in parentheses).
[b] N = 3.
[c] N = 1.

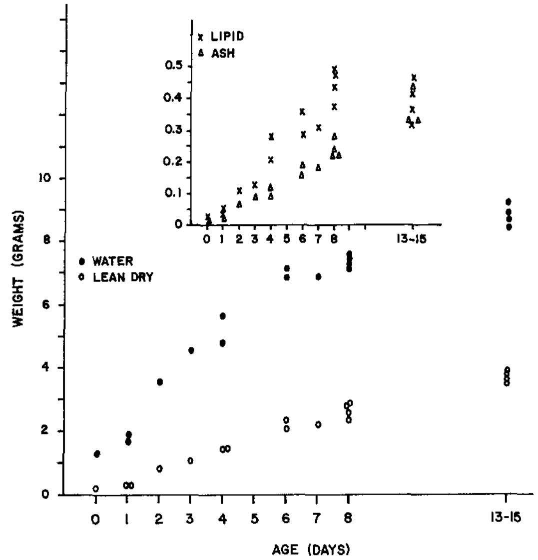

FIGURE 2. Increase in water, lean dry weight, lipid and ash constituents of the Rufous-winged Sparrow in relation to age.

(0.15–0.18, 4 nestlings on day 8). Fledglings aged 13–15 days exhibited the lowest fat indices (0.08 to 0.12).

Ash content increased slowly until fledging and then more rapidly as the skull became pneumatic and growth and mineralization of the bone was completed. The ash index decreased from 10.7 at day 0 to 6.6 at day 4, and then increased to 9.5 at fledging. The ash index of three adults was 11.4. The ash content of the bone increased from nil at hatching to about one-third adult level at fledging (8 days) and two-thirds adult level at two weeks (table 5). Mineralization apparently stopped then until after the first prebasic molt. Energy content (kcal/bird) and energy density (kcal/g wet weight) in-

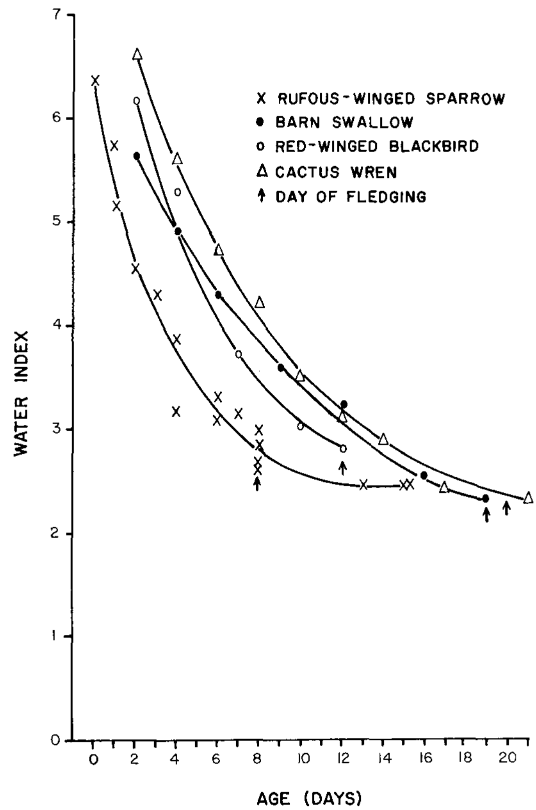

FIGURE 3. Comparison of water indices of four species of birds in relation to age.

TABLE 6. Allometric growth constants for body constituents.[a]

	Barn Swallow[b]		Cactus Wren[d]		Rufous-winged Sparrow		Bat (*Myotis thysanodes*)[f]	
water	(3–12) 0.90	0.81	(2–12) 0.91	0.84	(0–7) 0.91	0.87	(0–9) 0.91	0.79
	(12–18) –[c]		(12–adult) 0.33		(7–adult) 0.68		(9–adult) 0.66	
lean dry	(3–12) 1.22	1.33	(2–12) 1.36	1.52	(0–8) 1.34	1.40	(0–9) 1.30	1.40
	(12–18) –		(12–adult) 2.62		(8–adult) 1.79		(9–adult) 1.50	
lipid	(3–12) 2.16	2.60	(2–12) 1.15	1.10	(0–8) 1.60	1.40	(0–9) 3.00	2.06
	(12–18) –		(12–adult) 0.73		(8–adult) 1.40		(9–adult) 1.08	
ash	(3–12) 1.23	1.44	(2–11) 1.34	1.84	(0–4) 1.03	1.38[e]	(0–9) 0.95	1.42
	(12–18) –		(11–adult) 5.07		(4–adult) 2.09		(9–adult) 1.92	
energy content	(3–12) 1.42	1.65	(2–12) 1.30	1.39	(0–4) 1.39	1.39	(0–9) 1.68	1.52
	(12–18) –		(12–adult) 2.02		(4–adult) 1.41		(9–adult) 1.35	

[a] Given for two growth periods as indicated and overall, hatching = day 0, ages in days.
[b] From Ricklefs 1968b.
[c] Barn Swallows decrease in total weight before fledging.
[d] From Ricklefs 1975.
[e] Includes ash content of only body, head, wings and legs (including also ash in liver, pectoral muscle and stomach values are: 1–4 = 1.05, 4–adult = 2.11, overall = 1.46).
[f] Data for juvenile bats from O'Farrell and Studier 1973; data for adult bats from Ewing et al. 1970 (19 August sample).

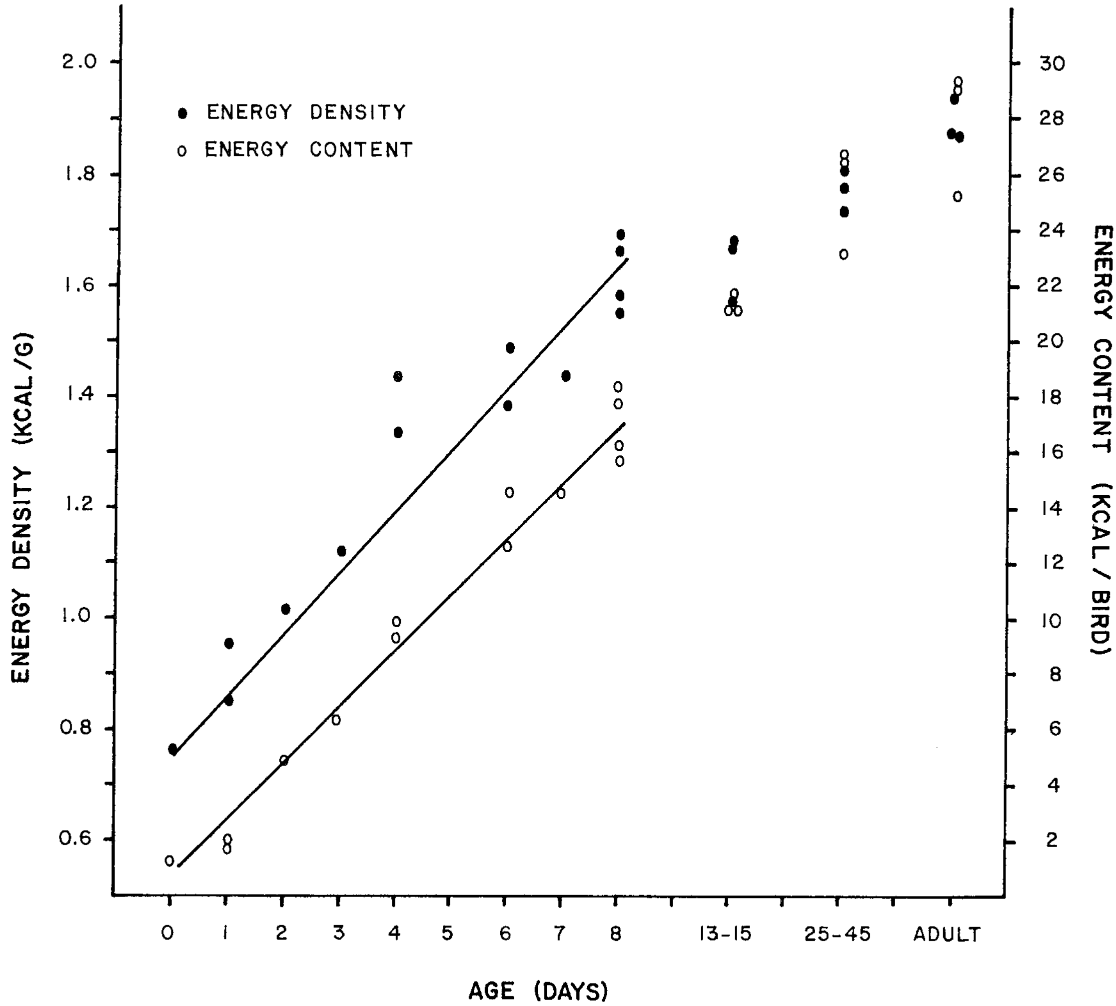

FIGURE 4. Energy density and energy content of the Rufous-winged Sparrow.

creased steadily through the entire growth period (fig. 4).

The rate of increase in weight of each constituent relative to the rate of increase in total weight was examined using allometric constants (table 6). Only the water constituent decreased relative to body weight (allometric constant less than 1.0). All others increased at nearly identical rates relative to body weight over the growth period as a whole. The lipid constituent increased more rapidly than other constituents during the nestling period but decreased relative to body weight after fledging. The lean dry and ash constituents increased more rapidly after fledging than before. The relative rate of increase in energy content remained constant throughout the growth period.

BODY COMPONENTS

Relative growth (allometric) constants of the body components of the Rufous-winged Sparrow indicate that each component has its own distinctive growth pattern (table 7). In general, components involved in locomotor and insulative functions grew relatively more rapidly than components involved in food processing.

Water indices for each component of the sparrow declined during development. Components related to functions fully developed in the hatchling (stomach, intestine, liver and heart) dehydrated rapidly to adult levels (fig. 5) and reached their asymptote about day 7; the pectoral muscles were still growing at fledging (fig. 6), by which time they had attained only 43% of adult weight.

BODY TEMPERATURE AND THERMOREGULATION

Mean body temperature (T_b) of nestlings in the nest increased gradually from about 35°C on day 0 to 40°C at fledging, with the range in body temperature decreasing from about

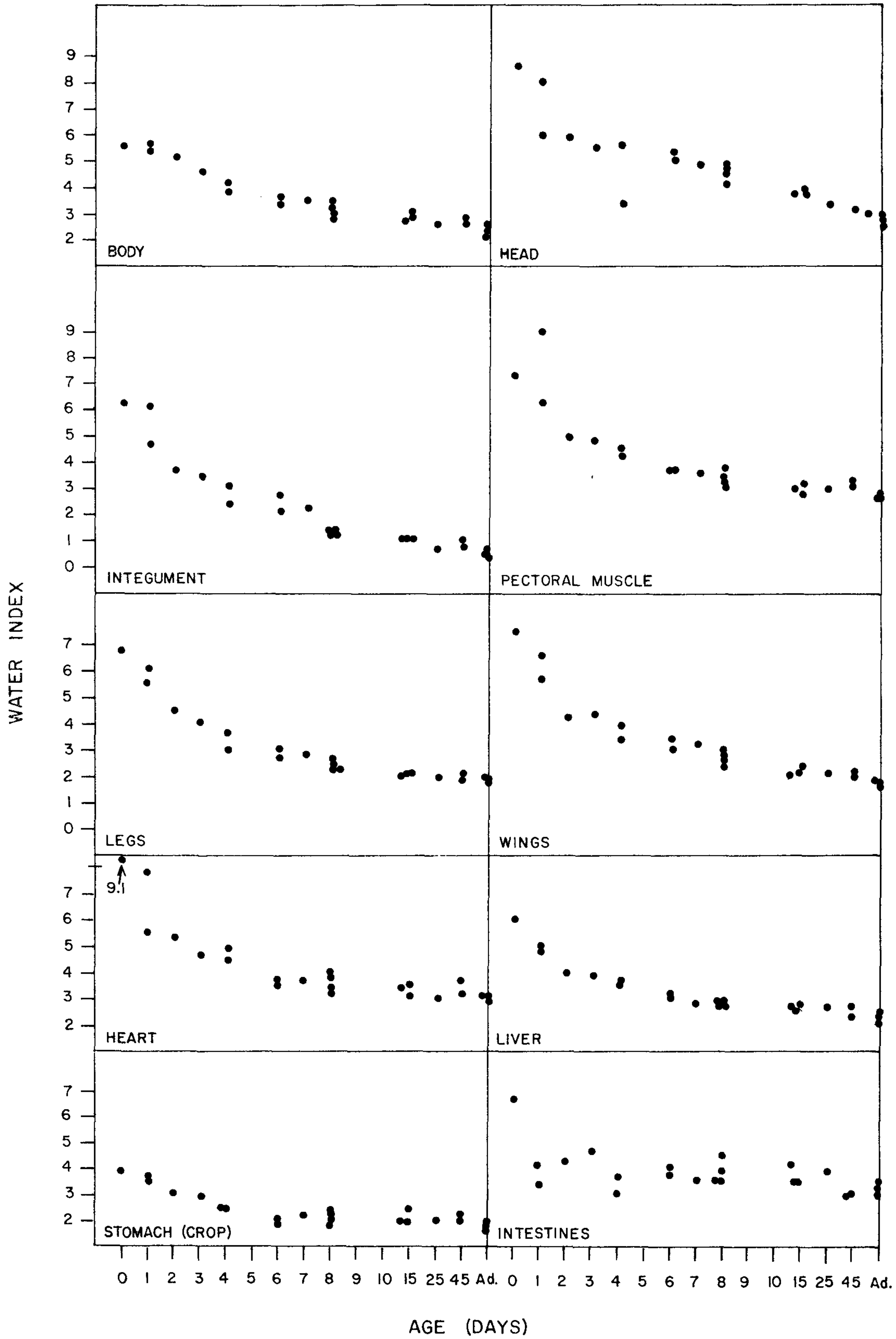

FIGURE 5. Decrease with age in the water indices of the body components of the Rufous-winged Sparrow.

TABLE 7. Allometric constants of growth of three species of altricial birds.[a]

Component	Redwinged Blackbird[b]	Cactus Wren[c]	Rufous-winged Sparrow
head	0.67	0.75	(0–4) 0.52; (> 4) 1.00; } 0.75
body	0.89	0.89	(0–8) 0.78; (> 8) 1.12; } 0.88
legs	1.21	1.21	(0–8) 1.12; (> 8) 0.40; } 1.03
wings	1.36	(0–10) 1.09; (10–14) 3.50; (> 14) 1.09; } 1.51	1.31
pectoral muscle	1.92	(0–10) 1.44; (10–30) 4.90; (> 30) 1.44; } 2.21	(0–6) 1.86; (6–8) 6.90; (> 8) 2.40; } 2.14
integument	1.34	(0–8) 1.60; (> 8) 0.64; } 1.26	1.21
liver	(0–3) 1.64; (3–12) 0.94	1.21	(0–3) 1.65; (> 3) 0.00; } 1.01
stomach	(0–3) 1.19; (3–12) 0.22	(0–8) 0.73; (> 8) 0.00; } 0.47	(0–8) 0.85; (> 8) 0.00; } 0.60
heart	1.02	(0–8) 0.62; (> 8) 1.22; } 0.93	0.84
intestine	—	0.58	(0–5) 1.58; (> 5) 0.00; } 0.95

[a] Where growth rates change, ages (in days) for each period are given.
[b] From Ricklefs 1967a.
[c] From Ricklefs 1975.

8 to 2°C (table 8). T_b increased slightly with increasing ambient temperatures in all age groups.

Elevation of T_b above ambient temperature after cold exposure first appeared on day 4 or 5 (fig. 7). Homeothermic capacity increased rapidly until day 8 when nearly adult levels were attained. Development of some body temperature control by day 4 was reflected in the sharp drop at this age in the percentage of time an adult was brooding when a nest was inspected (table 9).

TABLE 8. Body temperatures (°C) of nestling Rufous-winged Sparrows under natural conditions.

Age (days)	Ambient temperature (°C) 15–20	20–25	25–30	Body temperature $\bar{x}$	Range	N
0	34.7	35.3	35.6	34.9	6.7	24
1	35.9	35.4	36.4	35.8	8.3	42
2	33.6	35.5	37.8	36.7	8.0	42
3	36.7	37.6	39.0	37.6	7.3	41
4	37.1	38.2	39.4	38.1	6.3	36
5	38.4	39.0	39.7	39.0	3.8	27
6	39.1	39.2	40.1	39.4	2.7	23
7	35.5	39.2	40.4	39.7	3.6	27
8	39.3	39.9	40.6	40.1	2.0	14
9	41.0	40.0	–	40.5	1.7	5

DISCUSSION

Growth and development of the Rufous-winged Sparrow are similar to those of other fringillids (Dawson and Evans 1957, 1960, Maher 1964, Ricklefs 1968a, Yarbrough 1970, Morton and Carey 1971). During the first half of the nestling period, the heart, liver, intestine and stomach achieve most of their growth, and nearly all feathers appear above the skin. Subsequently, growth rate of most body components decreases, and the feathers begin to emerge from their sheaths and dehydrate, thus increasing insulation. Concurrently, temperature control becomes more refined until day 8 when a bird is capable of

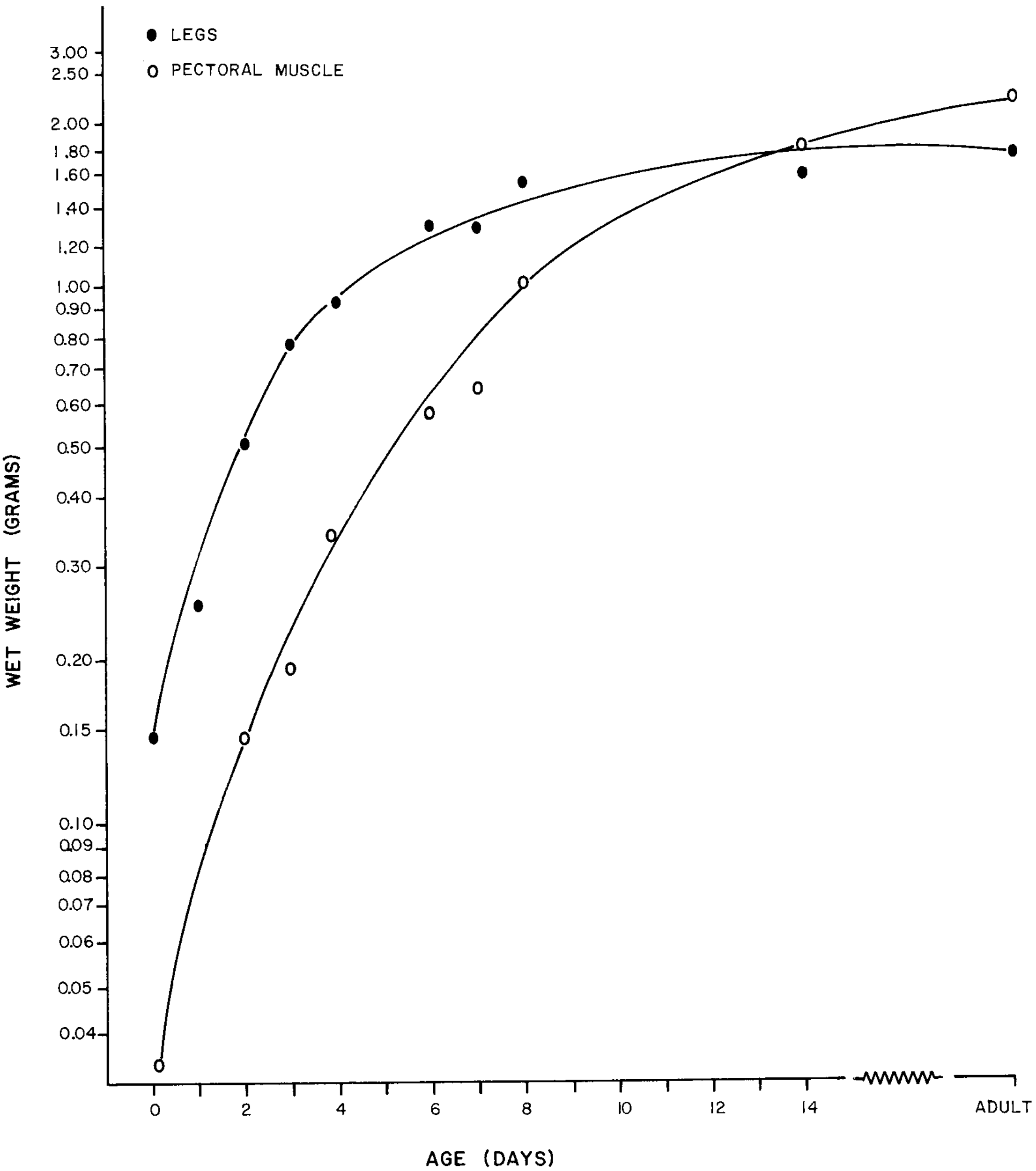

FIGURE 6. Growth of leg and pectoral muscle components as a function of age.

nearly adult levels of thermoregulation at ambient temperatures of 20–25°C.

The growth rate of the Rufous-winged Sparrow is geared to its short nestling period and rapid behavioral and physiological development (table 10). At fledging, certain components have attained nearly adult maturity, or a state equivalent to that of fledgling Cactus Wrens (table 11). At fledging, however, the sparrow is considerably less mature in most parameters than the wren. The two species are similar only in liver weight, leg weight, tarsus length, energy density, and thermoregulatory ability. Growth completed by the wren prior to fledging is delayed in the sparrow until after fledging, but is finished before the young are fully independent.

When young Cactus Wrens fledge (20 days), the tarsus, fleshy part of the wing, and most skeletal elements are fully grown; wing, primaries, and contour (central spinal tract) feathers are about 80% adult length, and rectrices about 60% (Ricklefs 1975). At 8–9 days (when Rufous-winged Sparrows fledge), these feathers of Cactus Wren nestlings have reached only 10–20% of adult length.

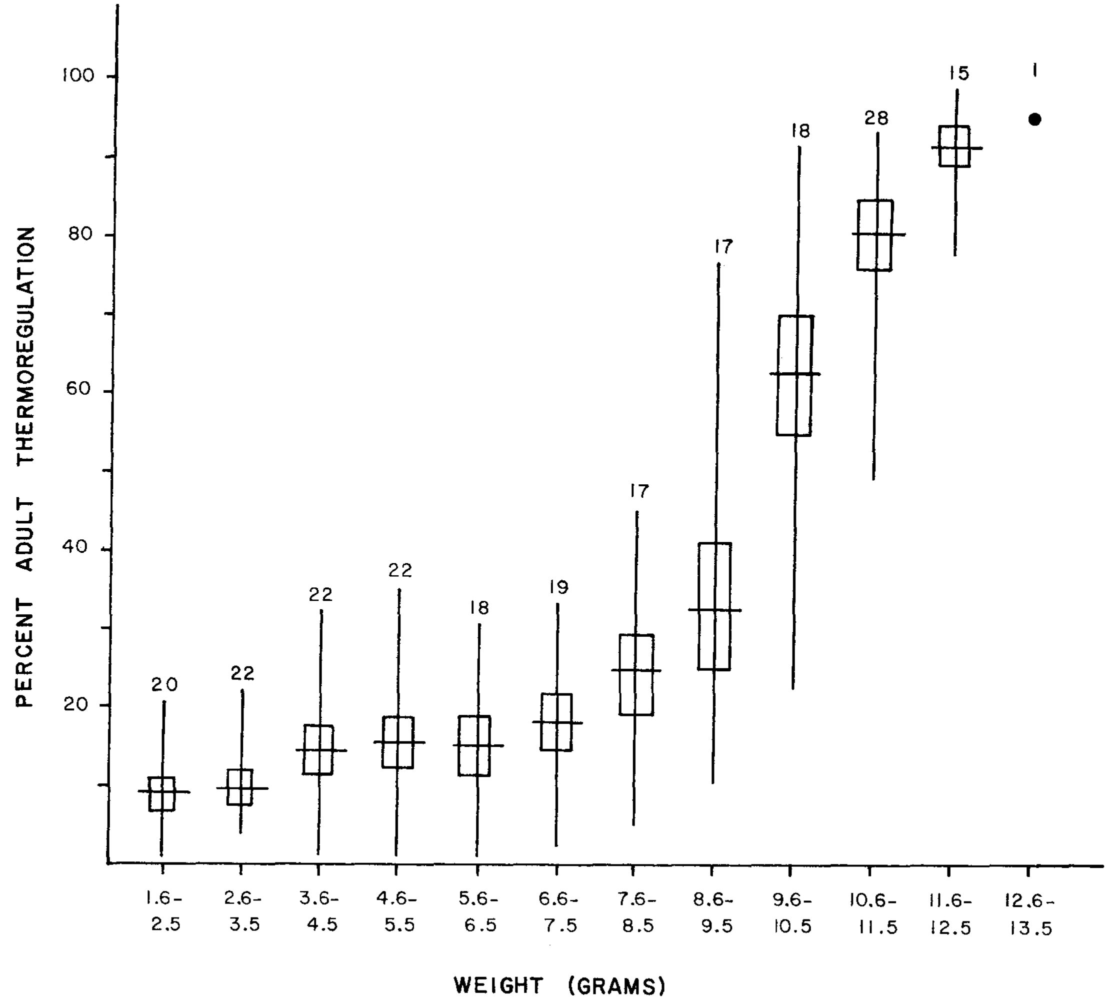

FIGURE 7. Development of thermoregulation (see table 9) in Rufous-winged Sparrows as a function of weight; data are mean horizontal line), range (vertical line) and 2 standard errors (open bar).

Sparrows can fly at about 12 days, 7 days earlier than young Cactus Wrens. Young wrens can fly weakly at fledging. At fledging, Rufous-winged Sparrows are about equivalent in development to Cactus Wren nestlings at 15 days of age. Conversely, wrens at fledging are as mature as sparrows which have been out of the nest for nearly a week (15 days old, table 11).

In contrast to the Rufous-winged Sparrow, the water content of both Cactus Wrens and Barn Swallows (*Hirundo rustica*) decreases before fledging (Ricklefs 1968b, 1975). The difference between the species is caused by the fact that the loss of water from maturing feathers and, to a lesser extent, other tissues, is offset in the sparrow by increase in weight of the body as a whole. In the wren and the swallow, feather maturation occurs after the nestlings have reached their asymptotic weight, and water loss is revealed by a decrease in total body weight. The relatively high water index at fledging is apparently a characteristic of species with a short nestling period. The Redwinged Blackbird (*Agelaius phoeniceus*) also fledges with a relatively high water index (2.8; Ricklefs 1967a), but two species with long nestling periods (Cactus Wren, Barn Swallow) fledge with water indices (2.4) approaching adult levels (Ricklefs 1967a, 1975).

The more rapid decrease of the water index of the sparrow compared to that of the wren cannot be explained solely by the rapid increase in body weight of the sparrow. When compared on a modified age scale (the growth index) which causes the growth curves to coincide, the water index of the sparrow remains below that of the wren throughout the nestling period, the two species converging only as they approach fledging (fig. 8). Cactus Wrens reach adult levels of the lean

TABLE 9. Development of body temperature control in the Rufous-winged Sparrow (temperatures in °C).

Age (days)	$\bar{x}$ Body temp. after cold exposure	$\bar{x}$ T_b-T_a after cold exposure	% Adult regulation[a]	N	% Time adult found brooding
0	21.3	2.1	9.1	20	59.0
1	22.2	2.8	12.1	33	58.1
2	22.3	3.2	13.8	34	58.3
3	23.0	3.9	17.3	34	44.4
4	25.2	5.5	25.1	30	17.5
5	30.9	11.0	50.4	18	19.4
6	36.5	15.8	74.9	19	16.1
7	39.2	19.4	87.4	18	11.7
8	40.1	20.2	92.4	9	10.0
9	40.9	21.8	95.1	4	–

[a] % adult regulation $= \frac{T_b-T_a}{42-T_a} \times 100$; adult body temperature assumed to be 42°C.

dry constituent at 40–50 days, apparently earlier than sparrows.

As in other species of passerine birds that have been studied, the lipid content of the nestling Rufous-winged Sparrow is low and consistent with findings on Cactus Wrens (Ricklefs 1975), but the fat index is similarly low in adults (0.07 to 0.12). The fat index of nestling Rufous-winged Sparrows at fledging is comparable to that of Redwinged Blackbirds but lower than that found in the Cactus Wren, and especially, the Barn Swallow (Ricklefs 1967a, 1975). Lipid indices at fledging may be related to degree of maturity at fledging and degree of post-fledging parental care. The decrease in ash index during the first part of the nestling period was also noted in the Cactus Wren and was attributed by Ricklefs (1975) to the decrease

TABLE 10. Comparison of developmental parameters of the Cactus Wren and Rufous-winged Sparrow.

Parameter	Wren	Sparrow
Growth constant (K)	0.394	0.576
Age at fledging (days)	19	9
Age at first (weak) flight (days)	19	12
Age at 50% adult thermoregulation (days)	10	5
% growth at 50% adult thermoregulation	76.2	63.3
% nestling period at 50% adult thermoregulation	52.6	55.6
Age at 80% adult thermoregulation (days)	11	7
% growth at 80% adult thermoregulation	80.5	73.2
% nestling period at 80% adult thermoregulation	57.9	77.8

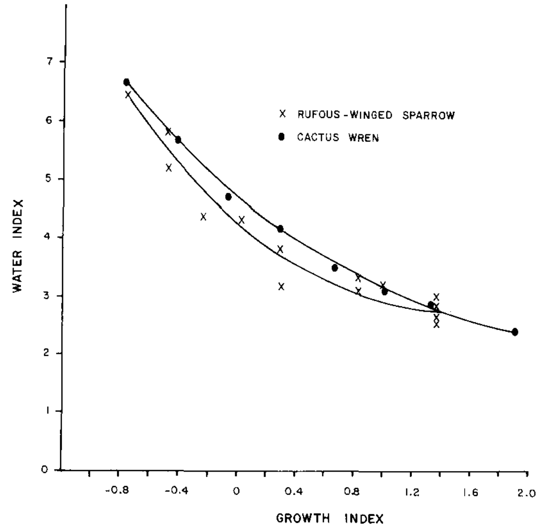

FIGURE 8. Water indices as a function of growth in the Rufous-winged Sparrow and Cactus Wren; the growth index, a modified time scale that is adjusted for growth rate, causes the curves for the body weight to coincide (Ricklefs 1967b).

in relative water content (and its dissolved salts) without concomitant mineralization of the bones.

Allometric rates of increase of constituents in the Rufous-winged Sparrow resemble those of the Cactus Wren, Barn Swallow and the bat, *Myotis thysanodes*, except for lipids (table 6). Lipid content of the Barn Swallow and, to a lesser degree, *Myotis* apparently increases more rapidly than in other species studied.

Relative growth constants of body components of Rufous-winged Sparrows resemble those of the Cactus Wren and Redwinged Blackbird (table 7). Head and body components exhibit similar allometric constants in the sparrow, blackbird, and wren. Pectoral muscle growth in the sparrow is similar to that of the wren in being relatively more rapid than that of the blackbird and having a phase of accelerated relative growth during the last half of the nestling period. The relative growth rate of the wings is similar to that of the blackbird but slower than that of the wren and without a pronounced phase of rapid growth. Relative growth of the leg and integument is less rapid than in either the blackbird or the wren. Relative growth of the stomach and intestine is more rapid than in the Cactus Wren, and that of the heart slower than in both the wren and blackbird. Relative growth of the liver is also slower in the sparrow than in the wren and blackbird. The liver of the sparrow attains

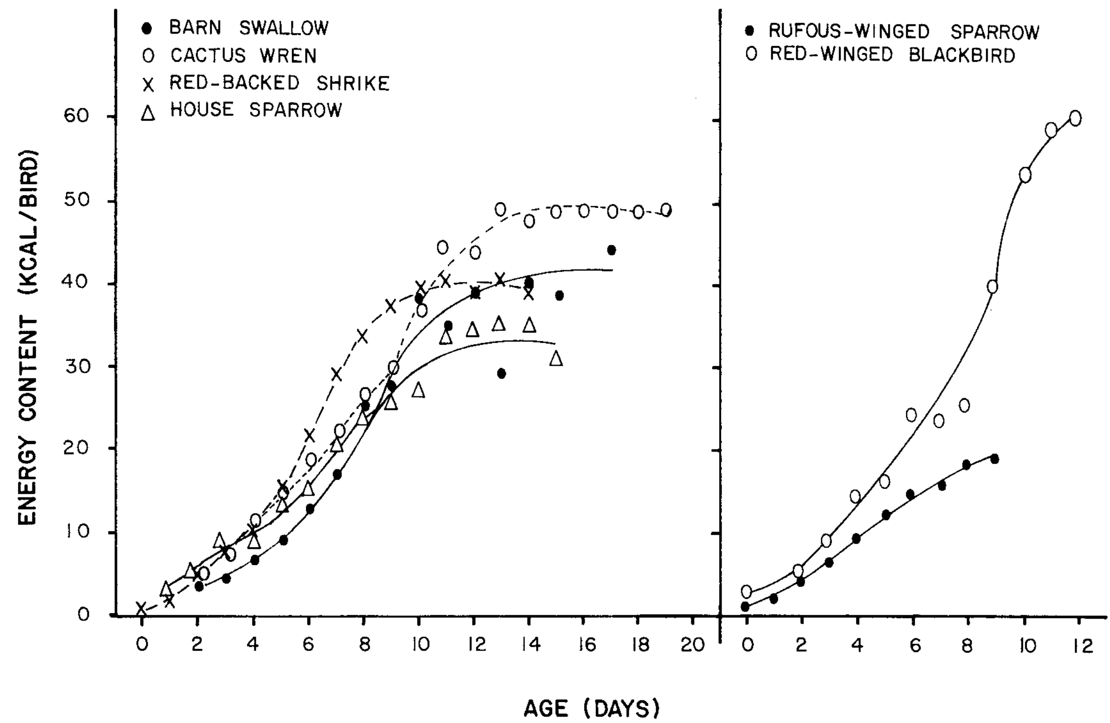

FIGURE 9. Increase in energy content of six species of passerine birds as a function of age.

adult size by day 4, and unlike that of the wren, does not exceed adult size during the nestling period. The relative growth of the heart and liver in the Rufous-winged Sparrow is also lower than in the Vesper Sparrow (*Pooecetes gramineus*; Dawson and Evans 1960).

The changes in allometric constants for those organs showing two growth phases occur at about day 4 in the Rufous-winged Sparrow, approximately the same age as similar changes in the blackbird, but considerably earlier than in the wren (7–10 days). The changes in relative growth rate do, however, occur at about the same point with respect to the body weight growth curve in the sparrow and wren (growth index for sparrow on day 4 = 0.302, for wren on day 7 = 0.287).

TABLE 11. Comparison of characteristics of Cactus Wren (CW) and Rufous-winged Sparrow (RWS).

	At hatching		At fledging		At 15 days	
	CW	RWS	CW	RWS	CW	RWS
% adult wet weight	9.6	13.1	88.7	77.8	85.6	88.9
% adult lean dry weight	6.8[a]	4.3	72.2	55.1	61.1	77.1
% adult ash	5.3[a]	4.0	66.7	46.0	46.4	66.7
% adult wing chord	8.5	10.0	87.5	68.0	67.0	87.0
% adult tarsus length	30.0	34.2	100.0	98.9	100.0	100.0
% adult primary length	0	0	83.5	70.1	64.0	87.7
% adult rectrix length	0	0	63.2	18.6	39.0	56.2
% adult bill length	24.0	27.4	74.6	65.8	64.2	—
% adult liver wet weight	25.0[a]	12.8	117.4	125.2	163.0	134.3
% adult heart wet weight	18.2[a]	11.2	100.0	69.5	100.0	88.1
% adult pectoral muscle wet weight	2.8[a]	1.4	69.4	42.7	46.2	73.7
% adult body wet weight	17.5[a]	13.2	94.6	76.9	90.9	88.4
% adult wings wet weight	12.1[a]	6.7	108.7	76.7	84.5	90.2
% adult legs wet weight	6.5[a]	9.1	79.5	79.9	73.1	86.7
% adult integument dry weight	2.9[a]	1.7	60.2	47.0	49.1	72.1
Water Index	6.6[a]	6.4	2.4	2.7	2.8	2.4
Energy density (kcal/g)	0.79[b]	0.76	1.76	1.62	1.64	1.63
% adult energy content	3.3[b]	4.6	67.9	66.4	—	76.9

[a] Age = 2 days (day 0 = hatching day).
[b] Estimated.

TABLE 12. Comparison of maturity at fledging of five passerines (LBMW = Long-billed Marsh Wren, BS = Barn Swallow, RWB = Redwinged Blackbird)[a].

	LBMW[b]	BS[c,d]	RWB[d,e]
Nestling period (days)	14	19	12
% adult wet weight	84.1	95.5	62.3
% adult lean dry weight	76.7	—	51.5
% adult ash content	62.6	—	—
% adult wing chord	—	79.8	55.4
% adult tarsus length	—	95.0	100.0
% adult primary length	—	82.1	59.3
% adult rectrix length	—	53.5	25.3
% adult bill length	—	—	77.1
Water Index	2.3	2.4	2.8
Energy density (kcal/g)	1.74	2.35	1.61
% adult energy content	79.0	—	—

[a] See table 11 for comparative data for Cactus Wren and Rufous-winged Sparrow.
[b] *Telmatodytes palustris*, from Kale 1965.
[c] From Ricklefs 1967a, unpubl.
[d] Adult linear measurements from specimens in the University of Nevada, Las Vegas collection.
[e] From Ricklefs 1967a, Holcomb and Twiest 1968.

The declines in the water indices of the body components of the Rufous-winged Sparrow are similar to those in the Cactus Wren although water indices tend to be lower in the developing sparrow at any age or point along the growth index scale (fig. 6). The water indices of most blackbird components are intermediate between the wren and sparrow.

Endothermic control of body temperature is attained rapidly in other fringillids (Dawson and Evans 1957, 1960, Maher 1964, Yarbrough 1970, Morton and Carey 1971), whereas in wrens, maturation of this function, with respect to both time and growth index, is delayed (Ricklefs and Hainsworth 1968).

From the available information, two basic patterns of development appear in passerines (table 12, fig. 9). Species with long nestling periods reach an asymptote of growth and energy accumulation several days prior to fledging and fledge at a relatively mature stage. Sparrows and other short-nestling-period species are less mature and are still growing and accumulating energy content in the tissue at fledging. The last quarter of the nestling period of species such as the Cactus Wren appears to correspond to the early post-fledging period of sparrows when maturation (decrease in water index, elongation and drying of feathers) is completed.

The short nestling period of the sparrow may be an adaptation to the relatively high nest mortality of finches compared to birds with longer nestling periods (Ricklefs 1969). Available data suggest that post-fledging mortality is lower than mortality in the nest (Ricklefs 1969). The rapid growth and development of sparrow-like birds may be the key to their success in unpredictable environments. A short development period allows several broods to be raised in a year and permits rapid replacement of young following unsuccessful breeding attempts. Similarly, this feature appears to allow these species to occupy certain specialized niches (e.g., Arctic, deserts with short rainy seasons) apparently unavailable to other species. Short developmental periods would seem adaptive where breeding seasons are brief, as in the Arctic or during the short period of summer rain which lasts as little as 2 months in the Sonoran Desert. Five of six species which breed only after the commencement of the summer rains in mesquite grassland in southern Arizona are fringillids. During each of two breeding seasons, Rufous-winged Sparrows were able to fledge two broods, and their production exceeded that of any other passerine (Russell and Austin, unpubl. data).

SUMMARY

The rapid growth and development of the Rufous-winged Sparrow are geared to its short nestling period (8–9 days) and are similar to those of other sparrows. In most aspects of development, this sparrow is considerably less mature at fledging than the Cactus Wren which has a long nestling period (20 days). In the sparrow only those functions necessary for survival out of the nest reach the level of maturity of Cactus Wrens at fledging. A developmental stage comparable to that of a fledging Cactus Wren is attained by the sparrow during the first week after fledging. We suggest that the short nesting period of sparows is an adaptation to high mortality rates in the nest and is a key to their success in habitats affording brief nesting seasons.

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