PATTERNS OF GROWTH IN BIRDS. III. GROWTH AND DEVELOPMENT OF THE CACTUS WREN

ROBERT E. RICKLEFS
Department of Biology
University of Pennsylvania
Philadelphia, Pennsylvania 19174

INTRODUCTION

This paper continues a comparative study of growth and development in birds by describing chemical and anatomical changes in the Cactus Wren (*Campylorhynchus brunneicapillus*) during the postembryonic period of development. Patterns of weight increase have been reported for many species (for reviews, see Ricklefs 1968a, 1973). Changes in body composition have been analyzed for some of these (Ricklefs 1967b, 1968b; Myrcha and Pinowski 1969; Brisbin 1969; Norton 1970; Dunn 1973; Brisbin and Talley 1973) in studies that deal primarily with energetic aspects of growth (Ricklefs 1974). Attempts to identify factors that could influence the evolution of growth rate suggest that the allocation of tissue to various organs and the degree of functional maturity of those organs—the basic organization of the body plan—may also influence growth rate (Ricklefs 1969). This study on the Cactus Wren is the first of a series of similar analyses of species with different rates of growth and development of mature functions (see Ricklefs 1973).

The Cactus Wren is representative of small altricial species with long nestling periods (21 days) and relatively slow growth rate (Ricklefs 1968a). The species was chosen for analysis because its nests are abundant and readily found. Moreover, while the young remain in the nest for about 3 weeks, fledglings stay in their parents' territory and sleep in roosting nests for more than a month after fledging. Therefore, young birds can be collected throughout the entire growth period. Anderson and Anderson (1961, 1973) give an excellent general account of the development of nestlings in their description of the life history of the species in Tucson, Arizona. Aspects of nestling behavior and the development of temperature regulation have also been studied (Ricklefs 1966; Ricklefs and Hainsworth 1968b, 1969).

Analyses of growth in the Cactus Wren are presented in the following order: (1) age and body weight growth; (2) increase in linear measurements of the body, limbs, and feathers; (3) increase in body constituents (water, lean dry weight, fat, and ash) with resulting changes in the percentage composition of the body and its caloric density; and (4) increase in weight of major body components and organs and their relative growth rates with respect to the body as a whole.

MATERIALS AND METHODS

Cactus Wrens were collected in Lower Sonoran Zone desert-shrub habitat, 10 miles east of Tucson, Arizona, at an elevation of about 2400 ft (see Ricklefs and Hainsworth 1968a). Nests of 25 pairs of wrens were found in one 75-acre area and others were located at scattered sites nearby. Young were collected for anatomical analyses from 25 of 67 breeding nests found. Nestlings were collected from early and late broods during April, May, and early June 1966. Broods that were eventually collected as fledglings were not disturbed during the nestling period.

Thirty-seven nestlings, whose ages ranged from 3 to 18 days, and 19 fledglings, aged 22–49 days, were processed completely. External measurements were made on 10 adults collected from roosting nests in 1966 but because these birds were held captive for other experiments, they were not processed. A series of free-living birds was shot on 12 July 1966 after the end of the nesting season, but only 2 of 20 specimens were adult. Additional adults were trapped at breeding nests during 6–9 June 1969 in the same study area. Specimens were usually frozen within 1 hr of collection.

Before processing, frozen specimens were thawed at room temperature and weighed. Appendages and representative feathers were then measured. Specimens were dissected in a cold room (4°C) to minimize water loss through evaporation. In this study, as much as 7% of the weight of specimens smaller than 10 g was lost during processing; about 1–2% was lost from birds weighing more than 30 g.

Specimens were dissected into component parts in the following order: (a) *integument*; (b) *head*, cut at its base; (c) *wings*, cut at the shoulders; (d) *pectoral muscles*; (e) *heart*; (f) *liver*; (g) *stomach*, from the posterior end of the esophagus to the exit of the small intestine (stomach contents removed); (h) *intestines*, with associated membrane, small organs, and fat deposits (contents not removed); (i) *legs*, cut at the hip; (j) remainder of the *body*, including kidneys, lungs, and other minor organs. Components were placed in tared aluminum pans and covered with a damp paper towel until they were weighed to the nearest milligram.

Components were dried in a vacuum desiccator at 47.5°C for 3 days, which was sufficient to obtain constant weight. Dried specimens, with their tared aluminum weighing pans, were tied in cheesecloth bags and placed in buckets containing a 5:1 mixture

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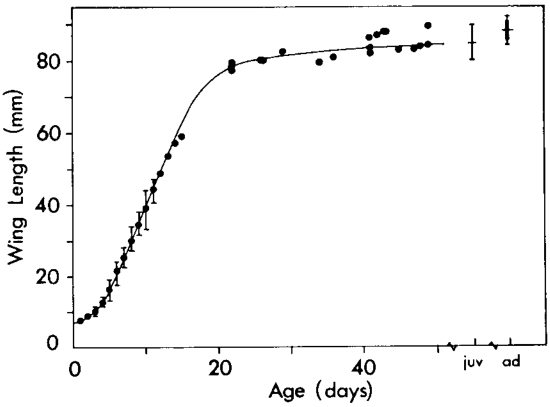

FIGURE 1. Increase in winglength from hatching to 50 days. Vertical lines represent ranges; data points between 20 and 50 days represent individuals; juv = unaged young of the year collected during July 1966; ad = 12 adults collected during June 1969, for which the standard deviation and range are indicated. The curve was fitted by eye.

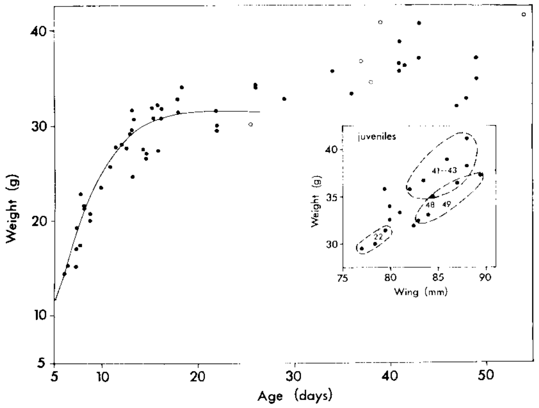

FIGURE 2. Increase in body weight from the early part of the nestling period to 50 days. The line represents the growth curve fitted to Anderson and Anderson's 1961 data; solid circles represent individuals used in the analyses in this study; open circles represent weights of juveniles reported by Anderson and Anderson (1962). Inset graph shows the relationship between weight and winglength for juveniles between 20 and 50 days old; individuals in three age groups (22 days, 41–43 days, and 48–49 days) are enclosed by dashed lines. Seven adults collected during June 1969 weighed an average of 35.5 g ± 2.84 S.D. (range, 32–41 g).

of petroleum ether and chloroform to extract fat. Components were transferred to fresh solvents after 24 hr where they remained for an additional 24 hr. Specimens were then dried in a vacuum desiccator at room temperature for 3–4 hr and weighed. Remains were combusted in a muffle furnace at 500–550°C for 24 hr to obtain ash content.

STANDARD GROWTH MEASURES

The body weights of nestlings in nine broods, in April 1966, closely matched the growth curve published by Anderson and Anderson (1961), so young were probably nourished normally during the period of this study. Winglengths of known-age birds were also measured to provide a standard curve by which other young could be aged when the date of hatching was not known. Because the range in winglengths for nestlings of the same age was similar to the daily growth increment for that age, winglength can be used to estimate chronological age to within 0.5 days for the first 2 weeks of the nestling period. In this study, nestling ages were estimated by the winglength-weight relationship, whether their chronological ages were known or not. The ages of all fledglings collected were known to within 1 day or less. The length of the wing increases rapidly during the nestling period and then more slowly for several weeks after fledging until adult length is attained (fig. 1).

Weights of specimens collected during this study are compared with the logistic growth curve fitted to Anderson and Anderson's (1961, 1973) growth data (see Ricklefs 1967a) in figure 2. Weights of nestlings level off at an average of 30–32 g during the last week of the nestling period. This plateau is considerably below the average weight of 38.9 g (range 33.4–46.9 g) reported by Anderson and Anderson (1973) for 42 adults, most of which were trapped between August and December. Seven adults collected in June during this study had an average weight of 35.5 g with a range of 32–41 g.

Juvenile Cactus Wrens slowly attain adult weight during the month after fledging (fig. 2). Variation in body weight among individuals of the same age during this period is closely related to variation in winglength (fig. 2, inset) and probably does not represent short-term nutritional deficits. Seven of 10 birds aged 40–50 days were collected on the same night, eliminating weather as a cause of weight variation. Juveniles aged 41–43 days weighed more than individuals aged 48–49 days because components of the younger birds contained more water. Loss of weight at this age therefore appears to be a significant developmental trend which will be discussed later.

INCREASE IN LINEAR MEASUREMENTS

The body frame and appendages (not including feathers or head) are fully grown by the time the young leave the nest, at about 20 days (fig. 3). Leg, tarsus, and upper arm measurements increase in parallel. Adult body length is approached earlier, which may

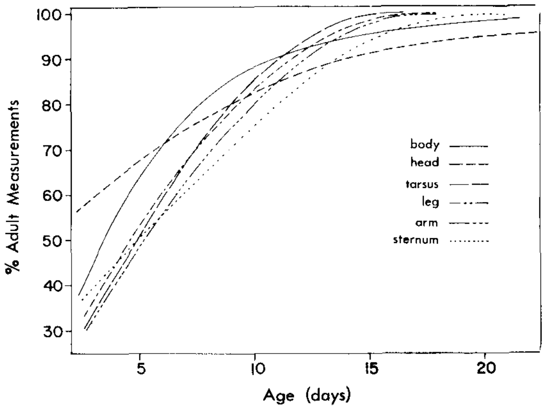

FIGURE 3. Increase in linear measurements of the body and its appendages expressed as a percentage of the adult measurement. Curves were fit to raw data by eye. Leg = knee to heel; arm = shoulder to elbow; sternum = base of furculum to posterior tip of sternum; all measured as straight-line distances on skinned carcass.

reflect the relatively large proportion of body weight that is allocated to visceral organs. Growth of the sternum lags behind the appendages by about a day, perhaps because the pectoral muscle mass develops somewhat later than the wing and leg musculature (see below). The head is about one-half adult length at hatching but increases more slowly than the rest of the body frame and appendages. The culmen stops growing shortly after young leave the nest but the culmens of juvenile birds (average length 23.4 mm, range 23–24) are significantly shorter than those of adults (27.5 mm, range 25–30, table 2, 1966 and 1969 combined).

Bone growth in the legs and wings is completed before the young fledge (figs. 4 and 5). The epiphyses of the long bones appear to become fused at 18 days. The epiphyses remained attached to leg bones after ashing on all specimens older than 18 days, but none younger. The attachment of the epiphyses correlates well with the completion of bone growth.

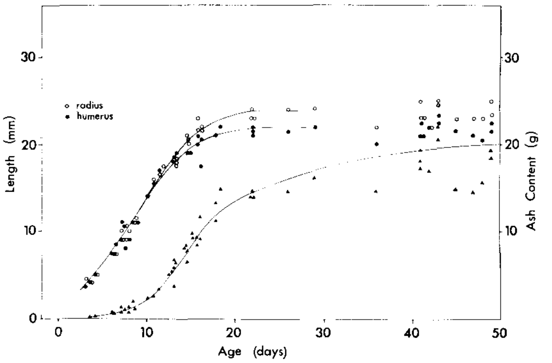

FIGURE 5. Elongation and ossification of the bones of the wing. Lengths measured on ashed specimens. Ash represents total in bones of wing component, including hand.

The mineral content of bones was calculated indirectly by subtracting an amount corresponding to the ash in soft tissues from the total ash of the wing and leg components. The ash content of soft tissues without bones (pectoral muscle, liver, stomach, and heart) averaged 1.9% of the water content of the tissue. The weight of ash deposited in bones was calculated by the expression, bone ash = total ash − (0.019 × water). Minerals were deposited in the bones more slowly than the bones increased in length. Mineralization was not completed until at least 30 days after hatching (figs. 4 and 5).

Except for the rectrices, feathers attain 80–90% of adult length by fledging (fig. 6). Primaries begin to break through their sheaths

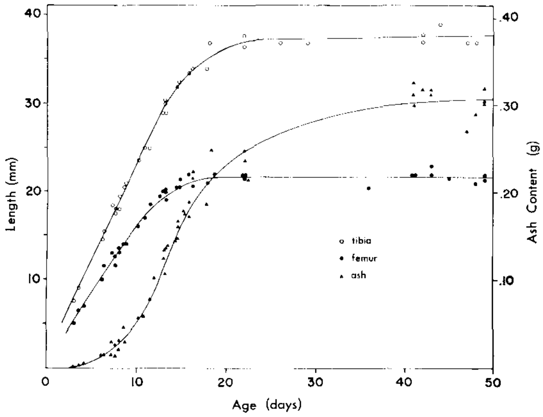

FIGURE 4. Elongation and ossification of the bones of the leg. Lengths measured on ashed specimens. Ash represents total in bones of leg component, including foot.

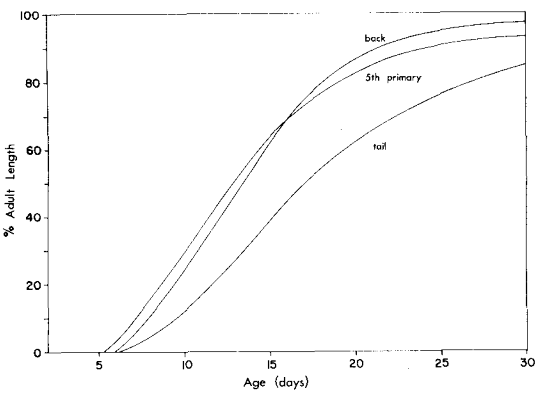

FIGURE 6. Growth of the 5th primary, inner rectrix (tail), and contour feathers from the central part of the spinal tract, expressed as a percentage of adult length.

TABLE 1. Linear measurements of adult and juvenile Cactus Wrens given as means, ranges, and standard deviations.

Group	Wing	Tarsus	Toe spread[a]	Culmen[b]	5th primary	Inner rectrix	Contour feathers[c]		
							Dorsal	Axillary	Ventral
Juveniles	85.3	28.4	44.9	23.4	66.5	76.2	27.1	16.1	13.9
40–49 days	82–89.5	27–30	41–48	23–24	63.5–70	73–79.5	24–29	14–18	11–15
(n = 11)	2.39	0.89	1.93	0.32	1.82	2.43	1.79	1.29	1.29
Adults	87.1	29.2	43.2	26.8	65.5	75.4	36.1	25.1	16.8
1966	85–91	27.5–30.5	42–46	25–28	62–69	72–78	32–38	17–31	14–19
(n = 8)	2.05	1.30	1.60	0.96	2.33	2.14	2.47	4.26	2.17
Adults	88.0	30.1	45.0	27.9	69.1	78.2			
1969	84–92	28–32	39–47	26–30	65–74	74–83			
(n = 12)	2.56	1.21	2.34	1.14	2.15	3.19			
Adult males	87.9	30.1	45.1	27.9	69.3	78.3			
1969	2.85	1.46	2.79	1.35	2.69	3.72			
(n = 7)									
Adult females	88.2	30.1	44.8	28.0	68.8	78.0			
1969	2.39	0.89	1.79	0.94	1.30	2.83			
(n = 5)									

[a] Tip of mid-foreclaw to tip of hindclaw.
[b] Measured from its base.
[c] Lengths are averages of several representative feathers from the same region of each bird.

at 8–10 days when they have attained about one-quarter of their final length. Primaries and rectrices of juveniles attain adult length but body feathers, though fully grown by 20 days, are shorter than corresponding adult feathers (table 1). As shown below, the integument of juvenile birds also weighs less than the integument of adults.

BODY CONSTITUENTS

The water content of nestling Cactus Wrens increases to an age of 13 or 14 days and then remains constant or decreases slightly during the last week of the nestling period, even though lean dry weight is still increasing at this time (fig. 7). The low water contents of several nestlings between 13 and 17 days of age are associated with low lean dry constituents. These individuals were probably undernourished.

After fledging, the water content of the nestlings increases gradually until it is about 10% higher at 40–50 days than during the last week of the nestling period. The postfledging increase parallels a gradual increase in the lean dry weight of the nestlings. Between 43 and 48 days, water content decreases in the absence of a marked drop in lean dry weight and lipid. Lean dry weight increases steadily and rapidly until about 18 days, after which growth continues slowly (fig. 7). The water content and lean dry weight of juveniles between 40 and 50 days of age falls within the range for adults collected during the summer months (water, 19.6–24.8 g; lean dry weight, 10.6–12.5 g).

Variation in lean dry weight of juveniles is related more closely to winglength (correlation coefficient, $r = 0.93$), which is presumably an index of the overall size of the individual, than to age ($r = 0.78$) (fig. 8). Lean dry weight and winglength are also correlated in a sample of adults ($r = 0.61$) and in a series of juvenile and immature wrens collected 12 July 1966 ($r = 0.74$) (fig. 8).

Lipids were not a major constituent of Cactus Wrens at any age. The fat index (fat divided by lean dry weight) varied widely without relation to age, between 0.1 and 0.3, during the nestling period (fig. 9). Fat indices of juveniles generally were below 0.15 and were about 0.05 in three individuals that had recently fledged.

The ash content of the body increases steadily during the nestling period and then less rapidly after fledging (fig. 10). The differ-

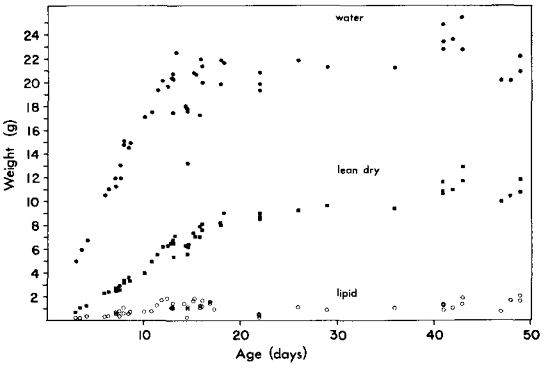

FIGURE 7. Increase in water, lean dry, and lipid constituents as a function of age.

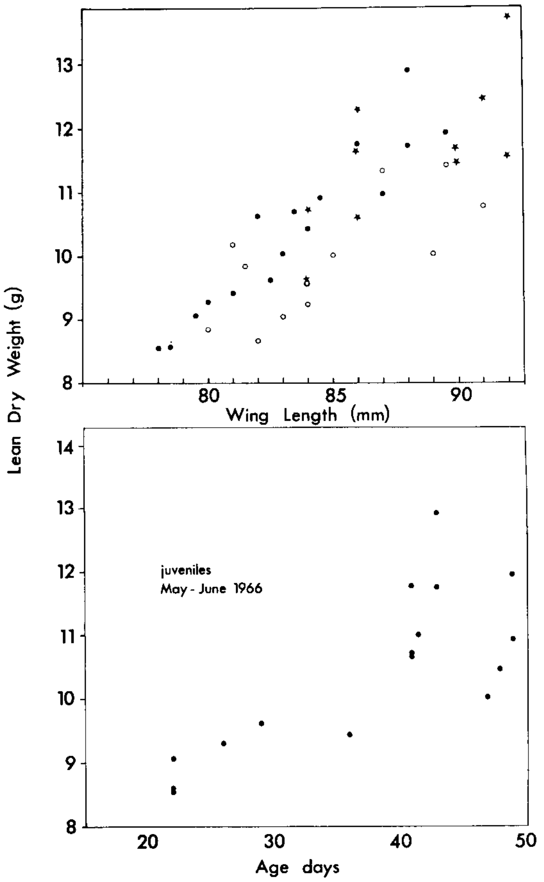

FIGURE 8. Relationship of lean dry weight to wing-length (above) and age (below). Open circles = juveniles, July 1966; stars = adults.

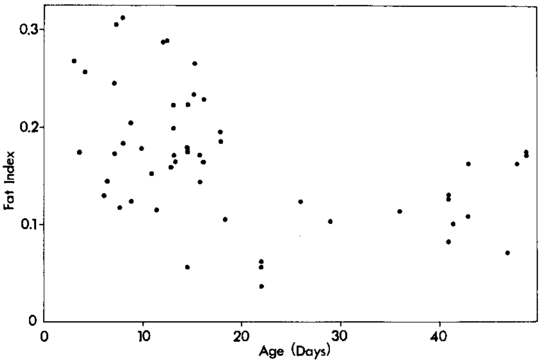

FIGURE 9. Fat indices (g fat/g lean dry weight) of nestlings (up to 20 days) and juveniles (21 days and older) as a function of age. The mean fat index of 12 juveniles and immatures in July 1966 was 0.130 (range, 0.091–0.160); that of 8 adults in June 1969 was 0.115 (range 0.057–0.196).

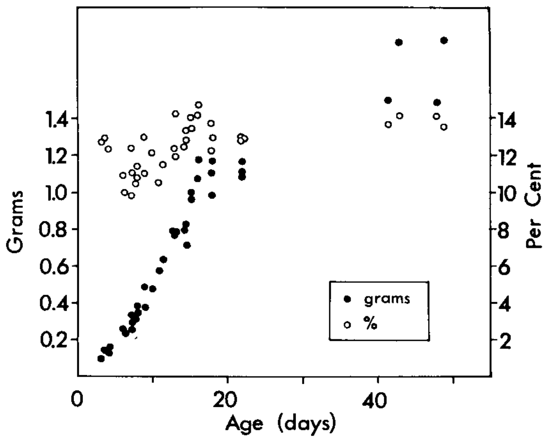

FIGURE 10. Total ash (solid circles) and ash content expressed as a percent of lean dry weight (ash index; open circles) of nestling and juvenile Cactus Wrens.

ence in ash content between 40 to 50 day-old juveniles (1.5–1.8 g) and two adults (1.85, 1.95 g) can be attributed partly to ossification of the skull, but other parts of the skeleton also become increasingly mineralized after 2 months of age (table 2). The 10–15% of the ash weight of juvenile and adult wrens located in the integument may represent an organic component, possibly melanin, because it was not soluble in hydrochloric acid.

The ash index (g ash/g lean dry weight) remains between 0.10 and 0.14 during the development period. It is slightly higher for adults (0.148 and 0.159 for two birds). During the early part of the nestling period, trends in the ash index are determined primarily by body water which contains about 1.9% by weight dissolved salts. Rapid mineralization of bones does not begin until about 10 days of age (compare figs. 4 and 5 with fig. 10). As the water index (water divided by lean dry weight) decreases during the first week of nestling life (see fig. 18), the ash index also decreases from about 0.13 to 0.10–0.11. As the bones ossify, the ash index increases, reaching 0.14 before the end of the nestling period. After fledging, loss of ash corresponding to reduced water index apparently balances gains by ossification, and the ash index does not change appreciably.

The accumulation of body constituents during the growth period can be expressed in energetic terms by converting lipid and ash-free lean dry weight (protein) to caloric equivalents: 1 g of lipid and 1 g of protein represent 9.5 and 5.7 kcal of combustible energy, respectively (Brody 1945; Kleiber 1961). Carbohydrates were considered to be insignificant. Odum et al. (1965) and Johnston (1970) empirically determined the caloric value of extracted lipids to be closer to 9.0 than 9.5 kcal/g, but this difference is not great enough to affect the general patterns in energy content described here.

The energy content of nestlings increases

TABLE 2. Ash content of body components.

	Ash weight (g)				
	Integument	Body	Head	Legs	Wings
Adults (2)[a]	0.182	0.491	0.316	0.492	0.232
	0.243	0.469	0.350	0.487	0.255
Juveniles (10)[b]					
mean	0.252	0.391	0.216	0.373	0.206
range	0.194–0.368	0.345–0.445	0.193–0.237	0.314–0.400	0.168–0.250
s.d.	0.067	0.035	0.015	0.028	0.027

[a] Collected July 1966.
[b] Ages 41–49 days.

more rapidly than body weight because energy density (kcal/g wet weight) increases as the water index of the young decreases (fig. 11). The increase in energy density in the Cactus Wren resembles that in other passerines (Ricklefs 1974). Most of the increase in energy density and total energy accumulation occurs before 15 days of age. Low values for 22-day-old fledglings reflect low fat content (see fig. 9). Energy content increases abruptly after 40 days when the dry weights of most components, especially the integument (see fig. 16), legs, and pectoral muscles, rise rapidly. Decreasing water content and water index between 43 and 48 days cause energy density to increase slightly during this period. Energy densities of two adults were lower than 48–49-day-old juveniles because the adults were less fat.

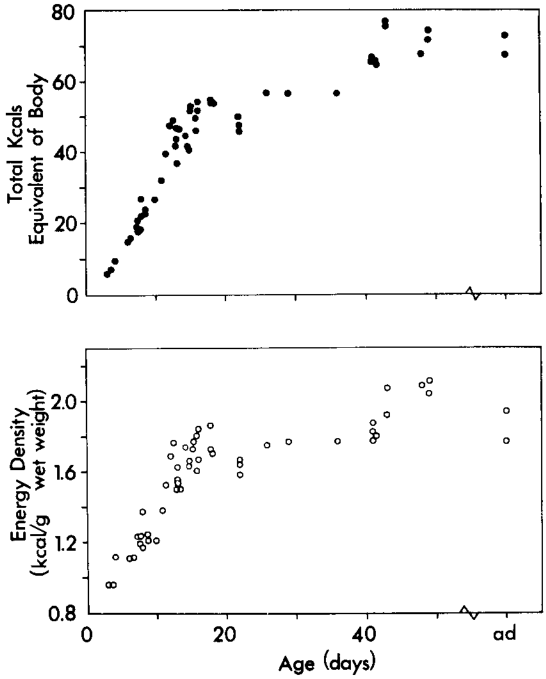

FIGURE 11. Total caloric equivalent (combustible energy; above) and energy density (below) of nestling and juvenile Cactus Wrens.

BODY COMPONENTS

Each organ or component of the Cactus Wren exhibits a distinctive pattern of growth and maturation. Organs associated with food-processing (stomach, intestines, liver) are large relative to their weight in the adult and

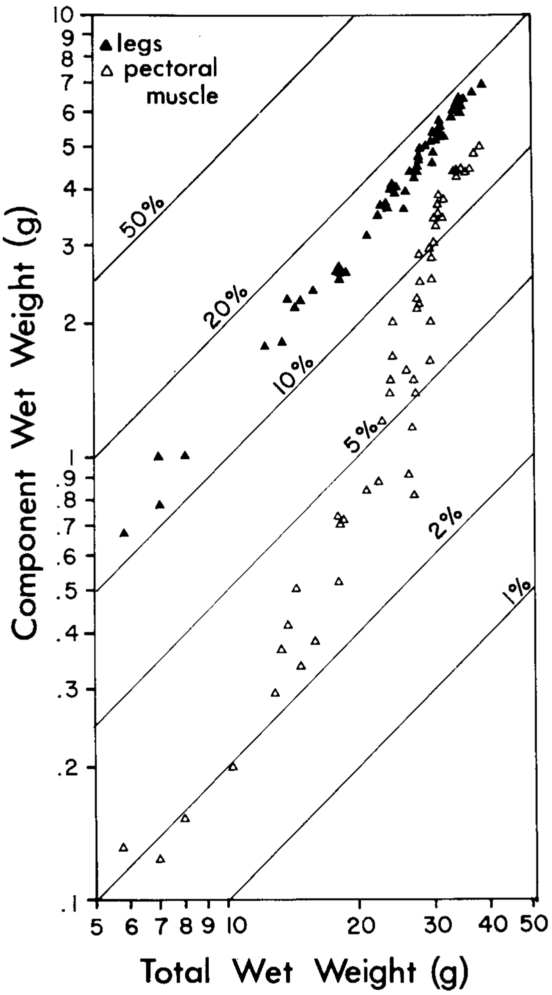

FIGURE 12. Logarithmic relationship between the lean wet weight of the leg and pectoral muscle components and the lean wet weight of the whole bird. The slope of the relationship is the allometric growth constant. Diagonal lines indicate percentages of total lean wet weight.

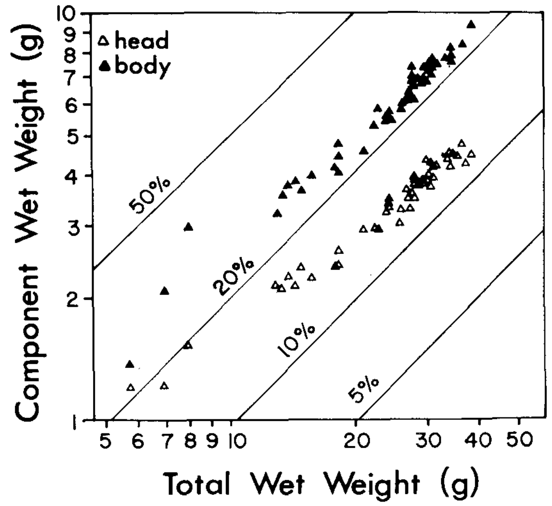

FIGURE 13. Allometric relationships of the body and head components to total lean wet weight, as in figure 12.

to the weight of the nestling at hatching; these organs grow relatively slowly during the posthatching period. By contrast, components associated with mobility (legs, wings, pectoral muscle, integument) are proportionately small at hatching and grow rapidly thereafter. This pattern is essentially identical to that described for the Red-winged Blackbird (*Agelaius phoeniceus*) (Ricklefs 1967b).

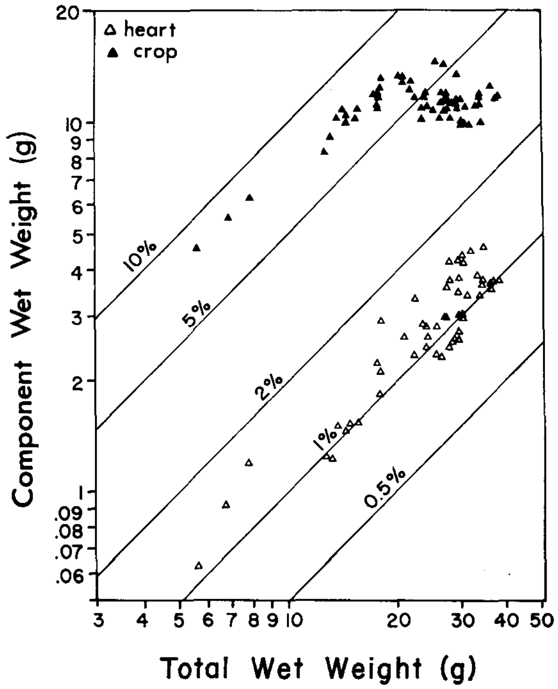

FIGURE 14. Allometric relationships of the stomach and heart components to total lean wet weight, as in figure 12.

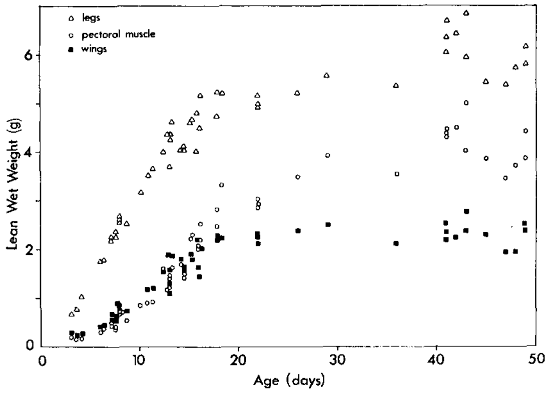

FIGURE 15. Lean wet weight of the legs, wings, and pectoral muscles as a function of age.

Logarithms of component weights are plotted as a function of the logarithm of the whole body weight in figures 12–14. The slope of this relationship is the allometric constant, which relates the growth rate of the organ to that of the body as a whole. Components that grow relatively faster than the body as a whole are characterized by allometric constants greater than 1. These components become a relatively larger proportion of the body with growth. If the allometric constant is less than 1, the opposite is true.

Allometric growth constants for the Cactus Wren are compared to those of the Red-winged Blackbird in table 3. Although the basic patterns of component growth in the wren and the blackbird are similar, differences can be related to the longer nestling period of the wren (20 days, compared to 12 days for the blackbird). The leg and body components have identical allometric growth rates in the two species, but the wings and pectoral muscles of the wren exhibit more rapid relative growth over the posthatching period as a whole. Phases of growth are arbitrarily delimited for the wing and pectoral muscle components in table 3. Relative growth rate actually changes more gradually, which can be seen for the pectoral muscle in figure 12.

Compared to the leg component, whose growth rate relative to the total bird is nearly constant throughout the posthatching period (fig. 12), the wing and pectoral muscles grow slowly until about 10 days, after which they increase rapidly (fig. 15). This phase of rapid growth of the wing component is briefer and less pronounced than that of the pectoral muscle, probably because the wing consists largely of bone and tendon, with relatively little flight muscle. Bone growth is completed by 18 days after hatching (fig. 5).

TABLE 3. Allometric growth constants of body components.[a]

Component	Weight range	Age at break (days)[b]	Growth constant	Overall[c]	Red-winged Blackbird
Body	entire	–	0.89		0.89
Head	entire	–	0.75		0.67
Integument	< 18 g		1.60		1.34
		8		1.26	
	> 18 g		0.64		
Legs	entire	–	1.21		1.21
Wings	< 22 g		1.09		
		10			
	22–27 g		3.50	1.51	1.36
		14			
	> 27 g		1.09		
Pectoral muscle	< 22 g		1.44		
		10			
	22–31 g		4.90	2.21	1.92
		ca. 30			
	> 31 g		1.44		
Intestines	entire	–	0.58		–[d]
Liver	< 20	10	1.21		1.64–0.94[e]
Stomach	< 18		0.73		1.19–0.22[e]
		8		0.47	
	> 18		0.00		
Heart	< 15		0.62		1.02
		7–8		0.93	
	> 15		1.22		

[a] When the slope of the relationship between organ weight and body weight changed, allometric constants were calculated for two or more arbitrary phases corresponding to these ranges in body weight.
[b] Age at which the allometric growth rate changes; because the changes are not abrupt, these ages are only approximate.
[c] The slope of a line drawn between the ends of the weight ranges, ignoring any curves in between.
[d] Included with the "body" component in the Red-winged Blackbird.
[e] A change in slope occurs at 3 days after hatching.

The relative growth constant of the integument of the wren decreases sharply from 1.60 to 0.64 at about 8 days after hatching. This change directly follows the onset of plumage maturation and the subsequent rapid decrease in the percentage water content in the integument. The primary feathers, for example, erupt from their sheaths at about 8–10 days. Although the wet weight of the integument decreases during the last week of the nestling period, the lean dry weight constituent continues to increase (fig. 16). The change in allometric growth constant for the lean dry weight of the integument, from 1.56 to 1.05 at about 10–11 days, is less abrupt than the corresponding change for the lean wet weight of the integument.

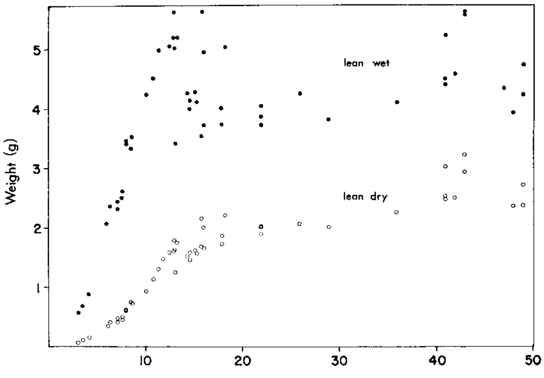

FIGURE 16. Lean wet weight and lean dry weight of the integument as a function of age.

Although the locomotory organs of the Cactus Wren grow relatively faster during the posthatching period than those of the Red-winged Blackbird, allometric constants for the visceral organs are somewhat lower (table 3). The liver decreases in weight during the last

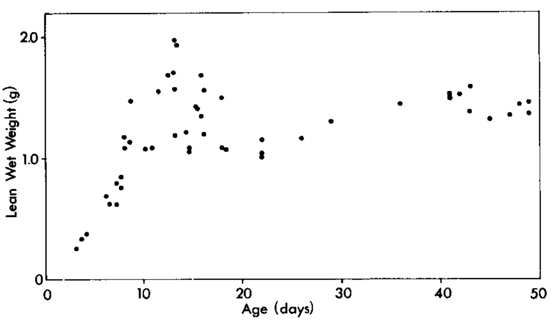

FIGURE 17. Lean wet weight of the liver as a function of age.

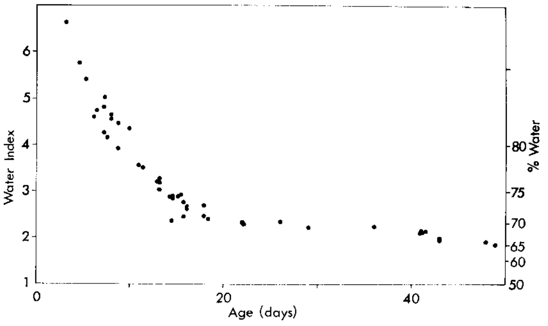

FIGURE 18. Water index of nestling and juvenile Cactus Wrens as a function of age.

half of the nestling period in the Cactus Wren (fig. 17), after rapid growth in body weight ceases. Atrophy may be associated with the declining need for synthesis of structural organic compounds, in which the liver plays an important role. The liver appears to enlarge again after fledging and it is half again larger betwen 30 and 50 days than in adult birds (0.86–1.06 g).

The proportion of water in tissues decreases as the tissues become increasingly functional. Water indices of nestling Cactus Wrens decrease through about the same range as nestling Red-winged Blackbirds and Barn Swallows (*Hirundo rustica*), from between 6 or 7 at hatching to about 2 at fledging (fig. 18). The water index of the blackbird, with a 12-day nestling period, drops off earlier by 2–3 days than either the swallow or the wren, with 20-day nestling periods. This difference is related to the earlier maturation of the blackbird. But the water index of the blackbird at fledging (about 2.8) is higher than that of either the swallow (2.3) or wren (2.3). Water indices of adult blackbirds and wrens are about 2.0 and 1.9, respectively.

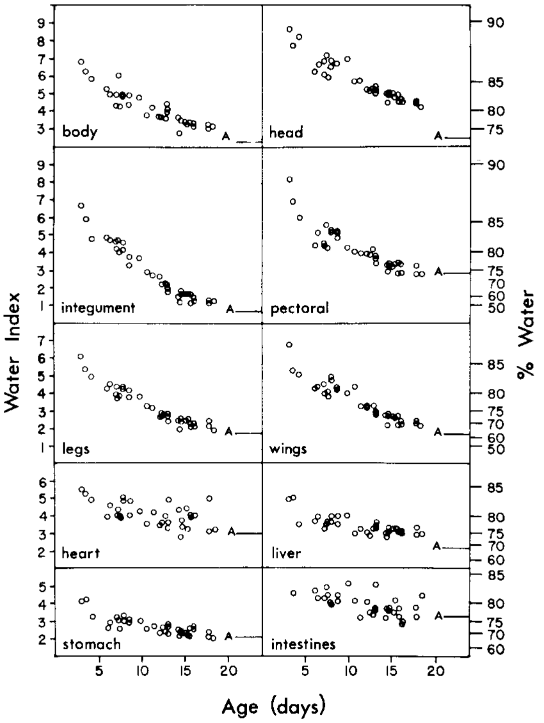

FIGURE 19. Decrease with age during the nestling period in the water indices of body components of nestling Cactus Wrens as a function of age. A = water index of component in adults.

Water indices of different components of the Cactus Wren decrease through different ranges of values during posthatching development (fig. 19). Again, the patterns are similar to those of the Red-winged Blackbird, but the decrease is prolonged. Water indices of components of adult birds vary from 0.6–0.8 for the integument to 1.7–1.9 for the wings and legs, which contain a high proportion of bone, to 2–3 for most of the visceral organs (table 4). The head is the only component, in both

TABLE 4. Weights of adult components.[a]

	Integ-ument	Body	Intes-tines	Heart	Liver	Head	Pectoral muscles	Legs	Wings	Stomach	Total
Water (g)	2.17	5.56	1.19	0.26	0.65	2.94	3.20	4.08	1.32	0.69	22.05
	0.25	0.70	0.17	0.04	0.05	0.16	0.38	0.37	0.15	0.14	2.02
Lean Dry (g)	3.22	2.34	0.37	0.08	0.28	1.13	1.09	2.20	0.75	0.32	11.78
	0.41	0.24	0.09	0.01	0.02	0.06	0.16	0.19	0.07	0.06	0.93
Lean Wet (g)	5.38	7.91	1.56	0.34	0.92	4.07	4.32	6.29	2.07	1.02	33.88
	0.67	0.96	0.25	0.05	0.06	0.23	0.54	0.58	0.20	0.20	2.95
Water Index[b]	0.68	2.36	3.34	3.15	2.37	2.61	2.87	1.85	1.77	2.07	1.87
	0.07	0.08	0.66	0.12	0.25	0.07	0.13	0.07	0.11	0.23	0.08
Lipid Index[c]	0.09	0.16	0.22	0.13	0.15	0.15	0.03	0.09	0.19	0.08	0.12
	0.05	0.08	0.08	0.04	0.04	0.03	0.04	0.04	0.03	0.05	0.05

[a] Eight individuals for all measurements except lean dry weight, for which 10 individuals were measured. Mean values and then standard deviations are presented.

[b] The water index is water/lean dry weight.

[c] The lipid index is lipid/lean dry weight.

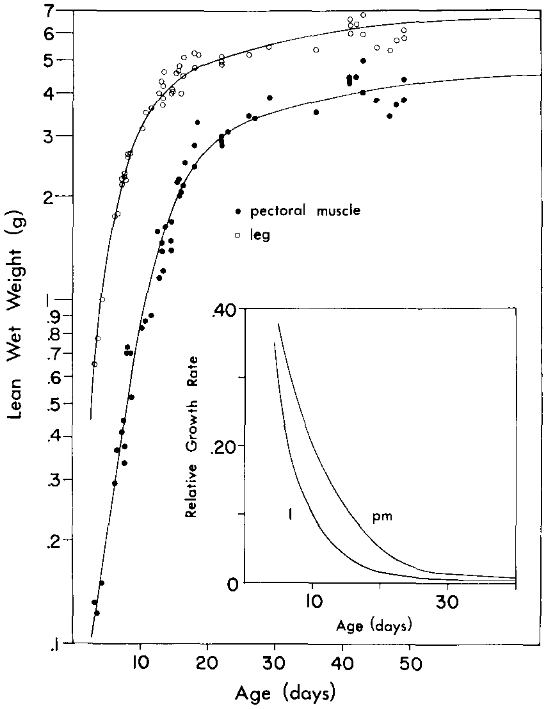

FIGURE 20. Lean wet weights of the leg and pectoral muscle components, plotted on a logarithmic scale, as a function of age. The slope of the growth curve, which is the relative growth rate (percentage rate of increase), is shown in the inset graph. L = leg; PM = pectoral muscle.

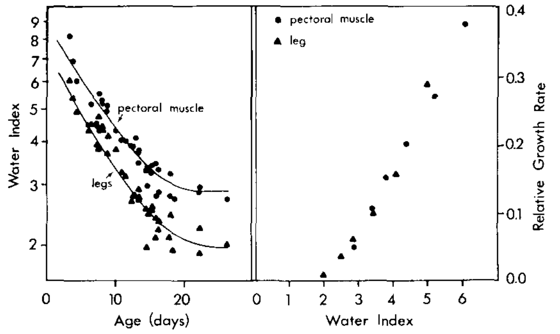

FIGURE 21. Water indices of the leg and pectoral muscle components of Cactus Wrens as a function of age (left); relationship between relative growth rate and water index (right).

the wren and the blackbird, whose water index does not closely approach the adult level before the end of the nestling period. In the wren, the water index of the head in adults lies between 2.5 and 2.7; values just prior to fledging are 4.2–4.6; between 22 and 26 days old, 3.7–3.9; and between 41 and 49 days old, 2.9–3.5. The prolonged decrease in the water index of the head parallels the relatively slow linear growth of the head (fig. 3) and its delayed ossification. The ash index varies between 0.18 and 0.21 just prior to fledging, between 0.18 and 0.19 at 22–26 days, between 0.20 and 0.22 at 41–49 days, and between 0.27 and 0.28 in two adult brids.

The timing of rapid growth of the locomotory organs varies according to the onset of function in the organs. Cactus Wrens do not fly until they leave the nest for the first time at 20 or 21 days although nestlings begin to flap their wings, as if to exercise them, several days before fledging. On the other hand, wrens use their legs from an early age to crawl from the nest cavity to the entrance, where they receive food from their parents (Ricklefs 1966). Size increase in the pectoral muscle is delayed with respect to the legs (figs. 12, 15, and 20), but the relative (percentage) rate of increase of the pectoral muscle is greater than that of the leg throughout most of the nestling period (fig. 20). Relative growth rates of the leg and pectoral muscle components are similar at 3–4 days: about 0.40, or 40% per day (inset in fig. 20). The more rapid decrease in the relative growth rate of the leg is directly attributable to its earlier maturation. The water index of the leg also decreases at an earlier age than that of the pectoral muscle (fig. 21). But when the relative growth rates of both components are graphed as a function of their water indices, the curves nearly coincide. This observation is consistent with a general hypothesis concerning variation in growth rate in birds (Ricklefs 1969, 1973) that differences in growth rate between components, between individuals of different ages, and between species are caused largely by differences in rate of maturation.

DISCUSSION

The development of the Cactus Wren closely resembles that of two other passerines that have been studied so far (Red-winged Blackbird and Barn Swallow). However, the earlier-fledging blackbird grows more rapidly and exhibits an earlier decrease in water index, indicating earlier maturation. Furthermore, allometric growth constants of organs indicate that the percentage composition of the body by component differs more at hatching from the adult in the wren than in the blackbird. Blackbirds thus appear to be better developed at hatching than Cactus Wrens, even though they have a shorter incubation period (12 versus 16 days).

Growth of the body frame and skeletal components of the appendages is essentially complete by fledging in the wren, but growth in weight continues for a considerable period beyond. The apparent leveling of the body weight growth curve prior to fledging is due to a decrease in water content, associated with maturation of tissues, while the dry weight continues to increase slowly (fig. 7). A second distinct phase of rapid growth may occur between 34 and 45 days and be terminated by a phase of maturation after 40 days. The water index finally decreases to adult levels at this time (fig. 18). Growth may be suspended (except for some plumage elements) between about 20 and 35 days, although the capacity for tissue growth is retained. Maintenance of the water index at a plateau that is substantially above the adult level during this period suggests that tissues are not fully matured and retain embryonic potential.

A prolonged period of weight gain in the Cactus Wren could decrease the energy, nutrient, or water requirements of nestlings and fledglings and enable adults to raise larger broods than if the young were to attain adult size rapidly. Weight gain is not completed until the young are at least partly self-feeding. Postfledging parental care is prolonged in the Cactus Wren compared to other temperate zone passerines. This extension of the family group may also permit the slower development of the young, particularly their locomotory ability. The adaptive significance of this growth pattern will undoubtedly become clearer as additional species with different growth rates and patterns of development are studied.

SUMMARY

Nestling, juvenile, and adult Cactus Wrens were analyzed to determine weights of body constituents (protein, water, fat, and ash) in each of 10 body components (various organs and tissues). Lengths of feathers and extremities were also measured. Cactus Wrens grow more slowly than most other temperate zone passerines. They also have a rather long nestling period (21 days). Body weight levels off at about 80% of adult weight during the nestling period. Adult size is attained within one month after fledging.

The skeletal frame and appendages are fully grown by 18 days after hatching, at which time the epiphyses of the long bones become fused to the bone shafts. Ossification lags behind increase in bone length and mineral accumulation in the bones does not level off until 30 days after hatching. All skeletal elements of juvenile birds contain less ash than those of adults.

Remiges and especially rectrices are not fully grown until well after fledging. Although contour feathers attain full length before fledging, the contour feathers of juveniles are shorter than those of adults; the integument of juveniles, as a whole, weighs less than that of adults.

Although total weight levels off during the end of the nestling period, lean dry weight continues to increase well after the young have fledged. Water content decreases slightly during the end of the nestling period, as the plumage dries and other tissues lose water with increasing maturity. After fledging, water content again increases, along with lean dry weight, until adult levels are attained. Fat does not play a major role in weight changes of the Cactus Wren.

The ash content, expressed as a percent of the lean dry weight, changes little during development. The tendency of the concentration of dissolved salts to decrease with decreasing percentage of water in the body is balanced by increasing ossification of the skeleton.

The energy content per gram wet body weight increases during the nestling period, as in other altricial species that have been studied, from less than 1 kcal/g at hatching to about 2 kcal/g at 15 days. Decreasing water content of the tissues causes most of this change.

Growth rates of body organs and tissues relative to the body as a whole are greater in components that attain mature function late in development (wings, legs, pectoral muscles, integument) than in components that attain mature function early (stomach, liver, heart, intestines).

Water indices (g water/g lean dry weight) in tissues at hatching are lowest in functionally mature components. The decrease in water index with development of function in the integument, legs, and pectoral muscles parallels that of the Red-winged Blackbird but occurs more slowly because the wren fledges, and thus acquires mature function, at a later age than the blackbird.

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