WEIGHT RECESSION IN NESTLING BIRDS

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It has been noted in many species of birds that the weight of growing young increases to a peak above normal adult weight and then decreases before fledging. This phenomenon of weight recession (Edson, 1930) has been attributed to various causes (e.g., drying out of the feathers, high energy demands with rapid feather growth, starvation periods, decrease in the size of the digestive organs) but little evidence has been sought to support any of these hypotheses.

This paper analyzes in detail the phenomenon of weight recession in nestling Barn Swallows (*Hirundo rustica*) and presents a general survey of the literature to determine the distribution of the phenomenon among avian groups.

MATERIALS AND METHODS

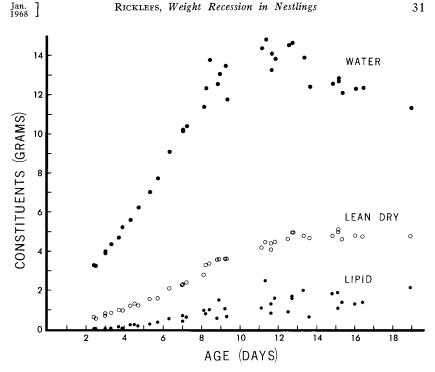
During the latter part of their 20-day nestling period the weight of young Barn Swallows decreases from an average peak of 20.5 g to 17.0 g (Stoner, 1935), a loss of 3.5 g. Adult weights in this species average about 18 g. To determine the nature of this weight change, a series of nestlings was collected in the vicinity of Philadelphia, Pennsylvania, and analyzed for water, lipid, and lean dry constituents. The 38 specimens ranged from 3 to 19 days in age and, with some variation, bore the same ageweight relationship described by Stoner. Ages were determined primarily from average growth curves of linear measurements, especially wing length, although nests were visited at least every other day. This method usually gives a more accurate estimate of a nestling's age than can be obtained from daily visits to the nest.

Thirty of the specimens were analyzed whole with the stomach contents removed, but the remaining 8, aged 9 to 19 days, were dissected into integument (skin and feathers), pectoral muscle, heart, liver, and stomach components which were analyzed separately. The whole nestlings and the components were dried in a vacuum desiccator and then extracted in a 5:1 mixture of petroleum ether ($30-60^{\circ}$ C) and chloroform to determine water, lean dry, and lipid constituents. All weights were measured on an analytical balance accurate to 1 mg.

RESULTS

The data on the constituents of whole birds (Figure 1) show that weight recession in nestling Barn Swallows can be accounted for entirely by a decrease in water content. The lean dry constituent exhibits no change after 12 days, when it levels off at about 4.8 g. Lipids vary considerably during the latter half of the nestling period but no decreasing trend is evident in the sample analyzed.

A more detailed account of these changes is given by component in Table 1. Loss of water is greatest from the integument but is also appreciable from the body and liver. The general trend of water loss from tissues is



Changes in body constituents of the Barn Swallow during nestling de-Figure 1. velopment.

documented in more detail elsewhere (Ricklefs, 1967). Changes in water content of the stomach and heart are negligible, but an increase in water of the pectoral muscles parallels an increase in the lean dry constituent. The lean dry weight of the combined body, head, and limb component does not change appreciably after the 12th day, but the liver undergoes a marked decrease in lean dry weight as well as water content after the 11th day. Even though the last week of the nestling period is a time of rapid feather elongation (Stoner, 1935) the lean dry weight of the integument does not increase appreciably. The slight decrease noted in nestlings G5 and K4 may be attributed either to individual variation or to the loss of feather sheaths.

WEIGHT RECESSION IN OTHER SPECIES

An extensive survey of the literature on growth in birds indicates that the phenomenon of weight recession is restricted primarily to oceanic species and to the swallows and swifts (Table 2). The magnitude of the weight recession, and of the increase in nestling weight above adult weight, is greatest in the petrels (Hydrobatidae) and shearwaters (Procellariidae)

	Individual									
Component	Age	G2 9.2	E4 11.1	I2 11.6	C3 11.6	C4 12.7	I4 15.1	G5 15.3	K4 18.9	
				Water						
Body, head, limbs Integument Pectoral muscles Liver Stomach Heart		7.31 3.25 1.01 1.18 0.57 0.21	7.25 3.54 0.97 1.94 0.51 0.25	7.73 2.85 0.95 1.83 0.55 0.24	7.58 3.19 1.23 1.21 0.49 0.21	8.24 3.18 1.40 1.14 0.53 0.24	7.22 2.11 1.55 1.09 0.57 0.23	7.37 1.91 1.22 0.96 0.47 0.23	7.03 1.27 1.66 0.67 0.59 0.19	
illuit		0.21				0.24	0.25	0.25	0.19	
Body, head, limbs Integument Pectoral muscles Liver Stomach Heart		1.76 1.08 0.25 0.33 0.19 0.05	1.92 1.31 0.26 0.53 0.17 0.06	Lean Dr 2.08 1.33 0.27 0.51 0.18 0.06	y 2.04 1.49 0.34 0.40 0.15 0.06	2.37 1.61 0.40 0.38 0.15 0.07	2.29 1.66 0.48 0.35 0.18 0.06	2.22 1.52 0.37 0.31 0.16 0.07	2.36 1.42 0.56 0.25 0.18 0.06	
				Lipid						
Body, head, limbs Integument Pectoral muscle Liver Stomach Heart		0.70 0.21 0.06 0.03 0.03 0.01	0.67 0.27 0.04 0.10 0.02 0.01	0.85 0.29 0.05 0.08 0.01 0.01	1.15 0.28 0.07 0.06 0.02 0.01	1.07 0.27 0.07 0.06 0.01 0.01	0.73 0.25 0.06 0.04 0.02 0.01	1.06 0.23 0.04 0.02 0.02 0.02 0.01	1.66 0.38 0.05 0.02 0.04 0.02	

TABLE 1
WATER, LEAN DRY, AND LIPID CONSTITUENTS OF COMPONENTS OF
BARN SWALLOW NESTLINGS ¹

¹ All weights are in grams. Ages of nestlings are in days after hatching.

and these are the only groups in which the relative loss of weight of nestlings is notably greater than in the swallows. Because of the magnitude of weight recession in species other than the swallows, there is no reason to assume that any mechanism other than water loss is responsible for the phenomenon except in the Procellariiformes. In this order accumulation of fat reserves and the subsequent "starvation period" noted by some authors (e.g., Harris, 1966) may add to both the peak nestling weight and the magnitude of the weight recession.

DISCUSSION

The phenomenon of weight recession in the Barn Swallow is related to changes in its water constituent during development. The water content of embryonic tissues, especially of the feathers, is known to be much higher than that of fully matured tissues (Ricklefs, 1967). This additional water in growing nestlings raises the body weight several grams above the adult level by the time the young are 10 to 12 days old. From then until the time of fledging, the maturing tissues lose water and weight recession ensues. During this period little change occurs in the overall lean dry con-

Family and species ²	Peak nestling weight	Fledging weight	Weight loss	Adult weight	Weight loss, per cen adult	t
	weight	weight		acigni	weight	
Spheniscidae	a 500 (fo)	2 100 (75)	600	2 100 3	206	Warham, 1963
Eudyptes chrysocome Procellariidae	2,700 (59)	2,100 (75)	600	2,100?	28.0	warnam, 1905
Puffinus puffinus	630 (50)	450 (70)	180	458	39.3	Harris, 1966
Hydrobatidae	000 (00)	100 (10)	100	100	0710	
Oceanodroma leucorhoa	69.5 (39)	36.0 (55)	33.5	44.1	76.0	Gross, 1935
Oceanodroma castro	74.8 (50)	48.6 (70)	26.2	43.5	60.3	Allan, 1962
Phaethontidae						
Phaethon aethereus	780 (80)	730 (100)		750		Stonehouse, 1962
Phaethon lepturus	400 (60)	330 (80)	70	300	23.3	Stonehouse, 1962
Sulidae						27.1 4074
Sula bassana	4,000 (65)	4 700 (100)		3,200	25.0	Nelson, 1964
Sula dactylatra	1,900 (80)	1,500 (120)		1,600		Dorward, 1962 Dorward, 1962
Sula leucogaster	1,400 (70)	1,140 (107)) 260	1,300	20.0	Dorward, 1902
Falconidae	194 (27)	185 (34)	9	184	4.0	Fowler, 1931
Falco columbarius Falco sparverius	194(27) 140(21)	133(34) 130(25)	10	111		Roest, 1957
Apodidae	140 (21)	130 (23)	10	111	9.0	Rocat, 1997
Chaetura pelagica	26.5 (21)	22.5 (33)	4.0	23.2	17.3	Fischer, 1958
Chaetura vauxi	21.0 (18)	18.5 (25)	2,5	19.2		Baldwin and
						Zaczkowski, 1963
Chaetura brachyura	20.5 (19)	15.9 (36)	4.6	18.3	25.2	C. T. Collins,
						pers. comm.
Cypseloides rutilus	26.0 (27)	24.0 (36)	2.0	20.0	10.0	C. T. Collins,
Apus apus	50.0 (27)	43.0 (40)	7.0	42.7	14.8	pers. comm. Lack and Lack,
		. ,				1951
Hirundinidae						
Tachycineta thallassina	21.7 (16)	17.0 (23)	4.7	14.8		Edson, 1943
Iridoporcne bicolor	21.8 (14)	20.0 (20)	1.8	21.1		Paynter, 1954
Progne subis	58.0 (18)	47.0 (31)	11.0	50.2	21.9	· · · · · · ·
Ct -1 - 1 - 1 + +	170 (12)	150 (10)	2.8	15.8	177	comm. Lunk, 1962
Stelgidopteryx ruficollis	17.8 (12) 18.6 (10)	15.0 (19) 15.7 (20)	2.8 2.9	15.8 14.3		Petersen, 1955
Riparia riparia Hirundo rustica	20.5(10)	17.0 (20)	2.9	14.3		Stoner, 1935
Petrochelidon pyrrho-	20.5 (12)	17.0 (20)	5.5	17.0	20.5	5,0101, 1905
nota	26.7 (15)	21.5 (23)	5.2	20.1	25.8	Stoner, 1945

TABLE 2

WEIGHT RECESSION IN NESTLING BIRDS¹

¹ All weights are in grams. Ages at fledging and attainment of peak nestling weights are given in parentheses.

² Families that do not exhibit weight recession and the number of species in each family for which growth curves were available are Phalacrocoracidae (2), Fregatidae (1), Ardeidae (2), Ciconiidae (2), Accipitridae (3), Tetraonidae (1), Phasianidae (2), Rallidae (1), Stercorcariidae (1), Laridae (1), Alcidae (2), Columbidae (3), Tytonidae (1), Strigidae (3), Trochildae (2), Picidae (1), and all families of the Order Passeriformes with the exception of Hirundinidae (45).

stituent, but some systems (primarily the musculature) are still growing, while others involved in food processing (e.g., the liver, and probably the intestines) are becoming smaller.

The phenomenon of weight recession has developed separately in several

orders (e.g., Sphenisciformes, Procellariiformes, Pelecaniformes, Apodiformes, Passeriformes, and weakly in some Falconiformes). The species that exhibit weight recession are similar in their well-developed flight capabilities at the time of fledging and their aerial foraging habits. These factors, and the changes in water associated with feather development, suggest a causal relationship between plumage development and weight recession.

The absence of high peak nestling weights and prefledging weight loss in a species could be due to 1) proportionally lighter plumage, 2) more staggered development of plumage elements, or 3) more precocious plumage development so that decrease in the water in feathers is concealed by increase in the weight of the remainder of the nestling.

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SUMMARY

Peak nestling weights above adult body weight and subsequent weight recession in Barn Swallows were found to be due to the high water content of embryonic tissues, especially feathers, and the loss of water during the maturation of these tissues. Swallows, swifts, and several families of oceanic birds are among the groups that have been shown to exhibit prefledging weight recession. Other groups that do not exhibit the phenomenon may differ in the relative weight of the plumage to that of body tissues and in the timing of its development.

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