

SOME QUANTITATIVE ASPECTS OF GROWTH IN THREE SPECIES OF BUTEOS

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The growth of nearly all diurnal birds of prey is inadequately defined. The pioneering work of Sumner (1929, 1933) is noteworthy, but most other growth data on raptors are spread throughout the literature, usually as unanalyzed presentations of cumulative growth curves. Even Ricklefs (1968), in his review of patterns of growth in birds, analyzed data for only a few raptors.

I recently examined the growth patterns of three congeneric sympatric birds of prey, namely, Red-tailed (*Buteo jamaicensis*), Ferruginous (*B. regalis*), and Swainson's Hawks (*B. swainsoni*), in the laboratory (see Olendorff 1971, 1972a,b for discussions of methods and other results). Emphasis was placed on the morphological aspects of growth, such as increases in body weight and the length of body parts; these data will be reported at a later date, after analysis of corresponding field data.

In the laboratory I also measured or calculated the following: (1) egg, eggshell, and hatching weights; (2) the difference in the timing of leg and wing growth; (3) food consumption (g of food consumed per bird per week); and (4) the percent efficiency of weight gain throughout the nestling period. These topics, the subjects of this paper, have practical application to research involving bioenergetics in raptors, captive breeding, and the physiology of growth.

EGG, EGGSHELL, AND HATCHING WEIGHTS

Data collected before and just after hatching of Red-tailed and Ferruginous Hawks are shown in table 1. After hatching and drying, the chicks (all birds combined) weighed 78% of the lowest egg weights taken within 6 days of hatching (range 75.4–83.0%). The eggshells and excreta (weighed as soon as possible after hatching) accounted for 13.6% of the egg weights (range 12.3–15.0%). The remaining 8.4% was lost by evaporation of water during hatching and drying of the young birds.

The average weight of 11 eggs for Red-tailed and Ferruginous Hawks combined was 67.1 g. The average weight of 11 hatchlings was 52.3 g, while 7 eggshells and the accompanying excreta averaged 9.2 g. The remaining 5.6 g was lost at hatching, presumably through evaporation.

The average body weights of the three species at hatching, calculated from all available data, were Ferruginous Hawks 51.6 g, Red-tailed Hawks 53.4 g, and Swainson's Hawks 39.4 g. Weights taken late in incubation for six Red-tailed Hawk eggs averaged greater (67.9 g) than the weights of five Ferruginous Hawk eggs (66.2 g). The Ferruginous Hawk may have smaller eggs (and smaller hatchlings) because it lays more eggs on the average than Red-tailed Hawks.

THE TIMING OF LEG AND WING GROWTH

Analysis of absolute day-to-day weight or length increase provides a method of analyzing original ob-

TABLE 1. Hatching data for Red-tailed and Ferruginous Hawks. All weights in grams.

Bird ^a	Date egg obtained	Wt. of egg ^b	Date egg hatched	Wt. of chick	Wt. of eggshell
R1	5/ 8/69	70.0	5/15/69	53.2	10.0
R2	5/ 8/69	68.0	5/16/69	54.5	9.9
R3	5/26/69	63.4	5/26/69	52.6	8.0
R4	5/20/70	70.7	5/24/70	55.7	9.0
R5	5/26/70	68.5	5/31/70	53.3	—
R6	5/26/70	67.3	6/ 2/70	50.9	10.1
F1	5/20/69	66.2	5/28/69	53.0	9.2
F2	5/20/69	66.6	6/ 1/69	51.5	8.2
F3	5/28/70	68.7	5/30/70	53.6	—
F4	5/28/70	66.9	6/ 1/70	50.5	—
F5	5/28/70	62.3	6/ 3/70	47.0	—

^a Key: R = Red-tailed Hawk; F = Ferruginous Hawk; # = individual.

^b Lowest weight taken within 6 days of hatching.

servations without making mathematical generalizations such as those required in curve fitting. [The results of curve fitting will be published elsewhere, but can also be found in Olendorff (1971).] The following information (see table 2) was derived from graphs of the day-to-day increases in the lengths of leg and wing segments of Ferruginous Hawks. Parallel analyses for the other species yield similar conclusions.

The wing segments reached maximal absolute growth in 8–10 days and remained at that maximal rate until the birds were 20–25 days of age. After day 25, there was a steady decrease to zero in the daily increments. Growth essentially stopped at 34 days of age in the brachium, 41 days in the antibrachium, 35 days in the manus, and 39 days in the wing as a whole. The middle wing segment required the longest time to complete its growth.

The relationships were different in the leg segments (table 2). Maximal absolute growth was attained earlier in the legs (5–8 days) than in the wings (8–10 days). The duration of the maximal growth period in the legs (6–8 days in length) was less than in the wings (10–15 days in length). The period of decreasing absolute growth was very short in the thigh and the third toe since the daily increments virtually stopped at 24–25 days of age. The middle leg segments (crus and tarsus), as well as the total length of the leg, stopped growing at 34–35 days of age. Note that the middle (and longest)

TABLE 2. Days of age when absolute growth or daily increments (DI) were maximal, and when absolute growth approached or first equalled zero for wing and leg segments of Ferruginous Hawks.

Limb segment	Age when DI maximal	Age when DI equalled zero
Brachium	8–20 days	33–34 days
Antibrachium	10–25 days	40–42 days
Manus	10–20 days	34–36 days
Winglength (total)	8–20 days	38–40 days
Thigh	5–11 days	23–25 days
Crus	8–15 days	33–35 days
Tarsus	7–15 days	34–36 days
Third Toe	5–12 days	24–26 days
Leg Length (total)	6–14 days	33–35 days

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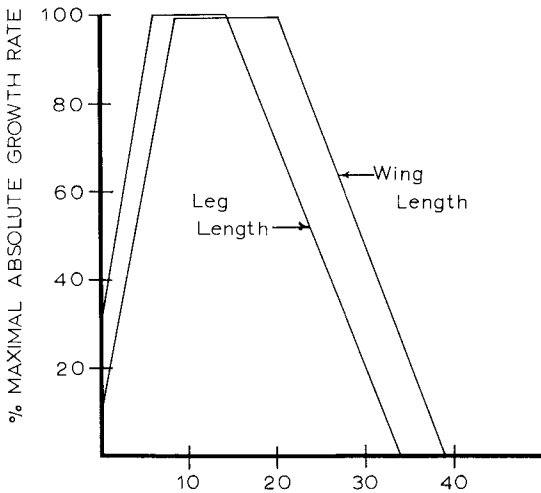


FIGURE 1. Generalized curves of absolute growth of total winglength and total leg length in Ferruginous Hawks.

segments of both limbs grew for longer periods of time than either the most distal or most proximal segments.

Thus the leg reached maximal absolute growth earlier, remained at maximal growth for a shorter period of time, and stopped growing earlier than the wing. This is shown graphically for total leg and winglengths in figure 1. Note also that the legs were growing at a greater percentage of maximal absolute growth at hatching than were the wings. The legs showed a spurt of growth soon after hatching and matured in function before the wings. The structures matured in the order in which they were put to use by the birds.

For five Ferruginous Hawks at hatching, the average total leg length (87.7 mm) was 25.5% greater than the average total winglength (69.9 mm); yet, at fledging, the winglength (408.9 mm) was 13.1% greater than the leg length (361.5 mm). This reversal was due to the prolonged period of growth at maximum rate in the wing. The wings and legs were growing further out of phase near the end of growth than at the time of hatching (fig. 1).

FOOD CONSUMPTION

Daily food consumption of Ferruginous Hawks, on a weight basis, plotted against days of age, increased steadily for 15–20 days, after which consumption was quite variable. After 25 days of age, food consumption showed a decreasing trend. This decrease is best shown by analyzing the amount of food eaten during each of the first 6 weeks after hatching. The total weight of food consumed by all birds of the same species during each week was calculated and then divided by the number of birds (fig. 2). Food consumption by Ferruginous and Red-tailed Hawks peaked during the fourth week, just before most measurements (particularly body weight) also peaked or began the slowing phase of growth. Food consumption by Swainson's Hawks peaked during the fifth week.

This trend in food consumption has been suggested by field observations. Schnell (1958) reported that young Northern Goshawks (*Accipiter gentilis*) he studied were fed less frequently as fledging neared. In a close study of several Cooper's Hawk (*Accipiter*

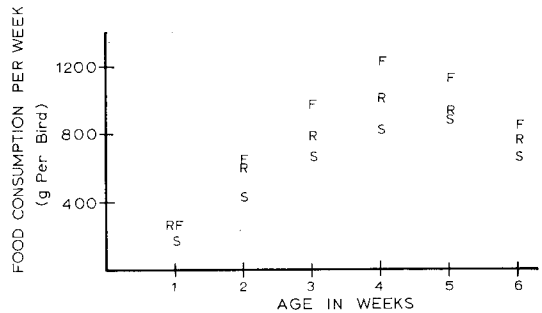


FIGURE 2. Food consumption per week (grams) of Ferruginous (F), Red-tailed (R), and Swainson's (S) Hawks during the first 6 weeks after hatching.

cooperii) nests, Meng (1959) determined a per-day count of prey items brought to the nests. The breakdown was as follows: "4 quarries per day during the first week, 5 per day during the second week, 7 per day throughout the third week, 9 per day during the fourth week, 7 each day during the fifth week and 6 per day in the sixth week. . . ." Meng's data on Cooper's Hawks support my findings for buteos.

The laboratory study carries the matter one step further in that the birds were systematically offered all the food they desired four or five times per day. The decrease in food consumption during the late weeks was evident nonetheless. This leads one to believe that the suggestion that young birds are starved to stimulate fledging may be incorrect or, at least, of relatively less importance than originally thought. The true decrease is apparently in the food consumption (metabolic demand) after the young birds reach maximum weight. Maximum weight is reached halfway to three-quarters of the way through the nestling period and corresponds with peak food consumption (fig. 2).

Another interesting calculation involving food consumption is the number of grams of food consumed per gram of hawk produced. This was calculated for the three species through 45 days of age. Ferruginous Hawks consumed slightly less than 4.7 g of food (range 3.6–5.3) per gram of asymptotic weight through 45 days of age. Red-tailed Hawks consumed slightly more than 4.7 g of food (range 4.2–5.4) per gram of hawk produced during the same period. Swainson's Hawks consumed over 5.7 g of food (range 5.4–6.6) per gram of asymptotic weight. The higher consumption by Swainson's Hawks probably reflects the inefficiency of smaller size due to relatively greater heat loss from small bodies. The difference in size between Swainson's Hawks and Red-tailed Hawks is greater than the difference between the latter species and Ferruginous Hawks.

PERCENT EFFICIENCY OF WEIGHT GAIN

Sumner (1933) described the growth of young raptors as follows: "(1) an initial period of rather slow gain in weight, . . . (2) a period of maximum increase in weight, . . . (3) a final and protracted interval of minor fluctuations. . . ." Sumner also offered a physiological explanation of his three-stage description of falconiform growth. He held that the initial period of slow weight gain was due to a condition of imperfect nutrition caused by the transition from yolk nourishment to feeding with meat. He speculated that this was a consequence of "breaking in" a relatively unused digestive tract.

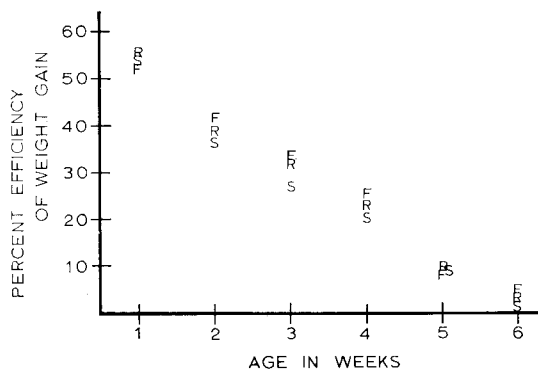


FIGURE 3. The percentage of food consumed (grams) which was converted to body weight (grams) during the first 6 weeks after hatching in Ferruginous (F), Red-tailed (R), and Swainson's (S) Hawks. % = body weight increase times 100 divided by food consumption.

An analysis of body weight increase per gram of food consumed (fig. 3) by the birds reared during this study does not support Sumner's conclusions. The highest efficiency of weight gain occurred during the first week of life and decreased throughout the growth period. Efficiency is here defined as the amount of weight gained per gram of food consumed. There was a slightly greater decrease in the percentage of food utilized for growth during the fifth week in all species studied. Body weight and most body parts began the decay phase of growth or reached asymptotes during the fifth week after hatching.

This research was supported by an NDEA Title IV Graduate Fellowship and a Graduate Teaching

COMMENTS ON THE SYSTEMATIC RELATIONSHIPS OF THE PIÑON JAY (*GYMNORHINUS CYANOCEPHALUS*)

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Relationships of the Piñon Jay (*Gymnorhinus cyanocephalus*) within the family Corvidae have never been studied in depth and still are not well understood. Recently, Hardy (1969), in his taxonomic revision of the New World jays, stated unequivocally that the Piñon Jay "is not a jay at all by any standard except that its plumage is blue in color. It is probably derived from Old World corvines such as *Nucifraga* (Hardy 1961:113) which it resembles except in color." Hardy apparently based this conclusion on one fact: Piñon Jays typically walk rather than hop. Other authors have concluded tentatively that *Gymnorhinus* is a New World jay (Ashley 1941; Amadon 1944; Pitelka 1951:205). Since a stated goal of Hardy's 1969 revision of the New World jays is to influence the format of the forthcoming revised A.O.U. *Check-list of North American birds*, it is thought worthwhile to present information which casts doubt on his views regarding the Piñon Jay.

COMPARISONS WITH OTHER CORVINES

Walking versus hopping. Walking is the only character used by Hardy (1961:113) to separate

Assistantship from the Department of Zoology, Colorado State University, and a Chapman Fund grant from The American Museum of Natural History. Certain computer analyses were performed by the staff of the Natural Resources Ecology Laboratory, Colorado State University, supported in part by National Science Foundation Grants GB-7824, GB-13096, and GB-38162X to the Grassland Biome, U.S. International Biological Program for "Analysis of Structure, Function, and Utilization of Grassland Ecosystems." Dean Amadon and James Grier read the manuscript critically.

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Accepted for publication 30 January 1974.

Gymnorhinus from other jays. Many passerines, including the Piñon Jay (Balda and Bateman 1971), which walk rather than hop as adults often hop as juveniles, suggesting that walking passerines are derived from hopping ancestors. The transition from hopping to walking is not a major "step." In fact, I often see walking and hopping in my captive Piñon Jays (typically a walker), Mexican Jays (*Aphelocoma ultramarina*) (hopper), and Clark's Nutcracker (*Nucifraga columbiana*) (hopper). The Mexican Jays walk when engaged in agonistic encounters. The nutcrackers hop almost exclusively. Furthermore, magpies (*Pica*) walk like crows, but are considered "garulines" rather than "corvines" by the A.O.U. Check-list (1957). These observations seem to negate Hardy's sole basis for concluding that the Piñon Jay "is not a jay at all. . . ."

Pterylography and molt. Thorough studies have been conducted on pterylography and molt of aphelocomine jays (Pitelka 1945), Clark's Nutcracker (Mewaldt 1958), and the Piñon Jay (Ligon and White 1974). Table 1 presents some comparisons of these three taxa. Both Pitelka and Mewaldt compared the species they studied with other corvids and the interested reader is referred to their papers for more general accounts of corvid pterylography and molt.

The presence of mid-dorsal apterium in both *Gymnorhinus* and *Nucifraga* is not of particular systematic significance, as it is present in *Calocitta* and *Cyanocorax chrysops* and is absent in *Aphelocoma*, *Cissilopha*, and *Cyanocitta* (Mewaldt 1958), all of which are unquestioned New World jays (Amadon