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# PHYSICAL DEVELOPMENT OF NESTLING BALD EAGLES WITH EMPHASIS ON THE TIMING OF GROWTH EVENTS

GARY R. BORTOLOTTI

Studies of avian growth have traditionally emphasized ontogenetic changes in body weight. However, the relative size and growth rate of different parts of the body have been useful in investigations of adaptive modifications of growth (e.g., O'Connor 1977, Ricklefs 1979a). In this paper I quantify the growth of flight feathers and various body components, and describe developmental changes in color and body contour feathers of Bald Eagles (*Haliaeetus leucocephalus*). Because growth rate is strongly associated with body size and mode of development (i.e., altricial or precocial) (Ricklefs 1968, 1973), the growth of Bald Eagles is of interest for it is North America's heaviest semi-altricial (Nice 1962) bird.

There is little quantitative information on the development of Bald Eagle nestlings. Very general descriptions of plumage changes, and some weight data, have been published for single (Stewart 1970, Gilbert et al. 1981) and a few (Herrick 1932) captive eagles. Bortolotti (1984a) presented growth data that can be used to determine the age and sex of wild Bald Eagle nestlings. Herein, I investigate the influence of sex on body size and feather growth, and how a chick's order in the hatching sequence within a brood may affect feather development. The timing of initiation of growth events will be a major consideration in assessing eagle development, as will both the absolute and relative growth rates. I also comment on parental nest attentiveness as it may relate to the thermoregulatory ability of the young.

## METHODS

Data on the growth of nestling northern Bald Eagles (*H. l. alascanus*) were collected from 1980–1982 at Besnard Lake (55°20'N, 106°00'W) in north-central Saskatchewan. Details of fieldwork will be brief for they are also described in Bortolotti et al. (1983) and Bortolotti (1984a, b). The study area is described in Gerrard et al. (1983).

I monitored the development of 64 nestlings, most of which were of known age, from 48 nests. Fifty-one of these birds were examined throughout most of the 10–12-week nestling period. I always recorded weight, length of the culmen (without cere), and length of the middle toe (without talon) for each nestling. When the chicks were about 2 weeks old (or as soon as measurements were possible, e.g., flight feathers) I also measured the depth of the bill at the leading edge of the cere, width of the tarsus, and length of the tarsus, foot pad, hallux claw, wing chord, eighth primary and central rectrix. Only three measurements were taken in the first 2 weeks because it was difficult or impossible to do otherwise given self-imposed time restrictions at the nest to limit the amount of disturbance to the birds. My method of measuring eagles is described in detail or diagramed in Bortolotti (1984a, c). Nestlings were handled an average of once every 6.7 days (usually every 5–8).

Because eaglets were not measured on day 0 (hatching) for all variables considered here, it was not possible to compare the average size of newly hatched chicks to their ultimate (asymptotic) size. However, data were available for a single bird. I collected an abandoned (naturally, not human-induced) egg which contained what appeared to be a fully developed embryo (Royal Ontario Museum 141311, in spirits) that would likely have hatched within a very short time. It closely resembles the embryo depicted in a photograph in Herrick (1932:432).

I graphically fitted individual growth curves (Ricklefs 1967) to data on weight and culmen length for 26 male and 21 female nestlings. I did not fit curves to data on each nestling for other variables either because the technique was not reliable given that early measurements were missing, or asymptotes were difficult to estimate. Instead, I applied the growth equations to the mean value per day of age for the depth of the bill, length and width of the tarsus, and length of the hallux claw and mid-toe for females. The analysis was only necessary for one sex because my purpose was to examine the relative growth of body components. To compare growth of body parts with different asymptotes, I calculated Ricklefs' (1967) growth index which replaces the time axis of the more usual growth curve. Growth is then expressed in units representing the time required to increase from 10–50% of the asymptote. Criteria for determining the sex of eaglets, and a comparison of nestling asymptotes to measurements of live mature Bald Eagles and study skins of eagles, are presented in Bortolotti (1984a).

I recorded the development of body plumage by noting the day the second down feathers emerged from the skin, and when feathers on various parts of the body first unsheathed and became noticeable. Because I did not inspect nestlings daily, feather development data were incomplete for some individuals. I also recorded the color of the eyes, skin, cere, culmen, gape, talons, and legs, but did not use a standard color chart.

I quantified the behaviors of nestlings and adults from tree-top and ground blinds situated near nests. Behavioral data presented here were based on 1131 h of observation of nine nesting attempts, three per year, from 1980–1982 (see Bortolotti 1982, 1984b; Bortolotti et al. 1983 for details).

## RESULTS

*Color.*—On the day of hatching, eaglets had dark brown eyes, the gape and legs were pink, and the skin was bright pink. The cere was very pale gray and the culmen was dark gray-black with a white tip. The talons were largely flesh colored. By day 1 the skin had faded to a soft pink, and the legs faded to a flesh tone. Beginning on day 2 and 3, but more usually on day 4 or 5, the skin became tinged with blue. Between day 4–8 the skin turned from largely pink to largely blue except for a small area under the wings. When the eaglets were 4–8 days old, the cere was pale yellow, the bill was dark gray-black, and the legs were pink-yellow. From 9–12 days the cere was pale olive, and the legs were pale yellow with some areas still pink-yellow. When 13–17 days old the legs were pale yellow, the cere was medium gray, and the culmen was very dark gray-black. The

TABLE 1
PARAMETERS OF GOMPERTZ EQUATIONS FOR WEIGHT AND CULMEN LENGTH GROWTH OF BALD EAGLES

| | | | Growth parameter | | |
|---|---|---|---|---|---|
| Variable | Sex | N | $K$ $\bar{x}$ ± SD (range) | $t$ $\bar{x}$ ± SD (range) | $a$ $\bar{x}$ ± SD (range) |
| Weight | M | 26 | 0.0683 ± 0.00330<br>(0.063–0.077) | 20.85** ± 1.153<br>(18.2–22.8) | 4066*** ± 178.9<br>(3575–4500) |
| | F | 21 | 0.0683 ± 0.00403<br>(0.057–0.075) | 21.80 ± 1.297<br>(19.2–24.9) | 5172 ± 213.3<br>(4800–5600) |
| Culmen length | M | 26 | 0.0553 ± 0.00414<br>(0.047–0.062) | 6.97*** ± 0.972<br>(5.2–8.8) | 49.14*** ± 1.315<br>(45.5–51.0) |
| | F | 21 | 0.0538 ± 0.00506<br>(0.045–0.062) | 8.78 ± 1.325<br>(5.6–12.1) | 54.39 ± 1.074<br>(52.0–56.5) |

** Males are significantly different from females, ANOVA $P < 0.01$.
*** Males are significantly different from females, ANOVA $P < 0.001$.

talons darkened and became grayish at the junction of the phalanges and were light brown distally. Colors intensified during the 18–22 day period; the legs became a deeper yellow, the cere was medium-dark gray, and the bill, especially the lower mandible, was still darkening. The talons were blackish with a brown tip. I recorded no further color changes except an intensifying of colors in certain areas (e.g., legs).

*Weight.*—The relationship between egg weight and hatching weight for chicks has not been documented for Bald Eagles. For one egg artificially incubated by Gilbert et al. (1981), the chick weighed about 76% of the weight of the egg just prior to hatching. In my study one eaglet upon hatching weighed 71% (85 g) of the weight of its egg measured 2 days before. The average weight of Besnard Lake nestlings (91.5 g, SD = ±5.17, N = 6) measured on day 0 (but not necessarily at the time of hatching) was 79.9% of the weight of the average fertile egg (114.4 g, SD = ±10.59, N = 17) near the time of hatching. This is comparable to the results of Olendorff (1974) for Red-tailed Hawks (*Buteo jamaicensis*) (78.6%) and Ferruginous Hawks (*B. regalis*) (77.3%).

Table 1 presents data for the Gompertz growth equation parameters $K$ (a constant proportional to the overall growth rate), $t$ (the inflection point), and $a$ (the asymptote) for weight curves. The asymptotes were not correlated with the $K$ or $t$ values of either sex ($P$s > 0.05). However, $K$ and $t$ were highly significantly correlated for males ($r = -0.773$, df $= 24$, $P < 0.01$) and females ($r = -0.635$, df $= 19$, $P < 0.01$). Males were significantly smaller and had earlier inflection points than females, but were no

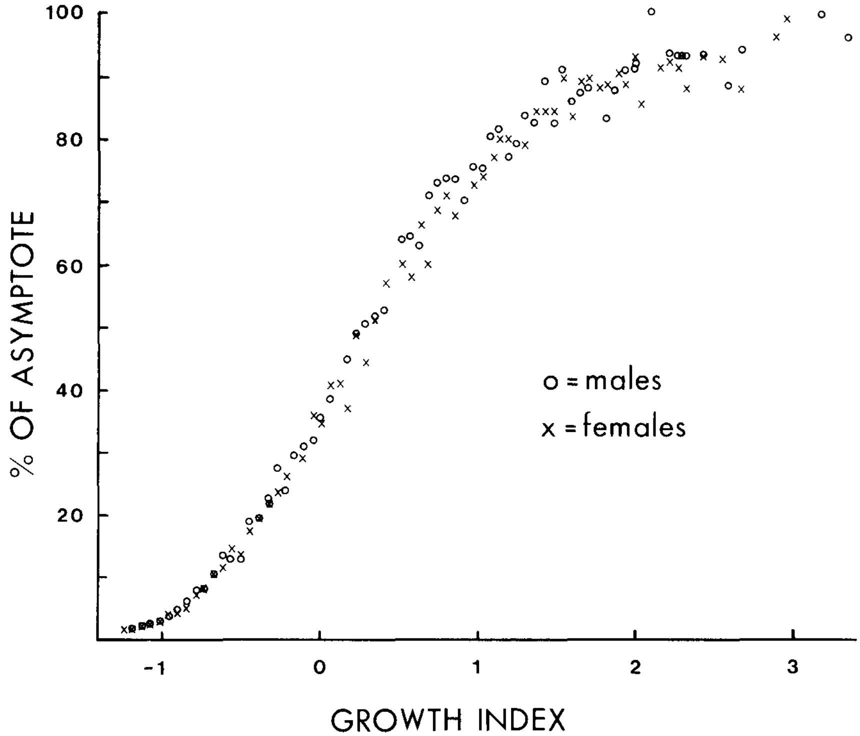

FIG. 1. The relative weight growth (percent of asymptote attained in relation to the growth index) for male (o), and female (x), nestling Bald Eagles. Points represent the mean weight for each day of age.

different in growth rate. However, when the average weight curves of the sexes were compared using the growth index, the relative growth of males and females was the same (Fig. 1).

Because of the Bald Eagle's large body size, daily weight gain can be substantial (up to 180 g/day, Fig. 2). The maximum rates shown in Fig. 2 are artificially lowered somewhat by the fact that each point represents the average gain over the 5–8 days between successive measurements. The absolute growth rate ($dW/dt$) for the Gompertz equation can be calculated by the formula:

$$dW/dt = -KaW(\log_e W)$$

where $K$ is the growth rate constant, $a$ is the asymptote, and $W$ is the fraction of the asymptote of the growth curve attained (Ricklefs 1967, 1968). At the inflection point of the growth curve ($W = 0.37$), when

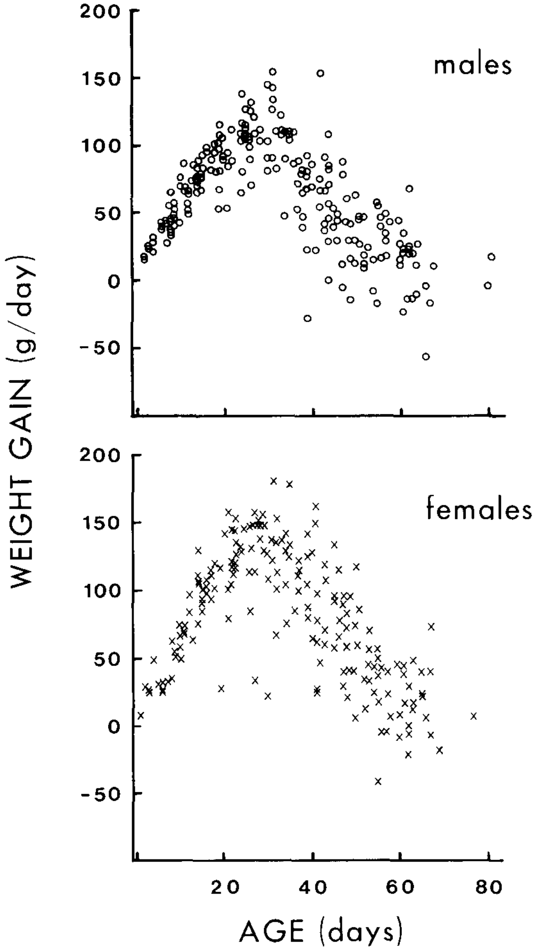

FIG. 2. Weight gain (g/day) as a function of age for male and female nestling Bald Eagles. Each point represents a single measurement.

maximum growth occurs, the average male and female Bald Eagle (Table 1) should gain weight at a rate of 102 and 130 g/day, respectively. The weight gain per day expressed as a percent of the total body weight on that day is illustrated in Fig. 3. The largest relative weight gains were early in the nestling period.

*Body components.*—Table 2 presents the absolute and relative size of an embryo near hatching. The body cavity is small, but the bill and legs are relatively large. This chick was small compared to most hatchlings.

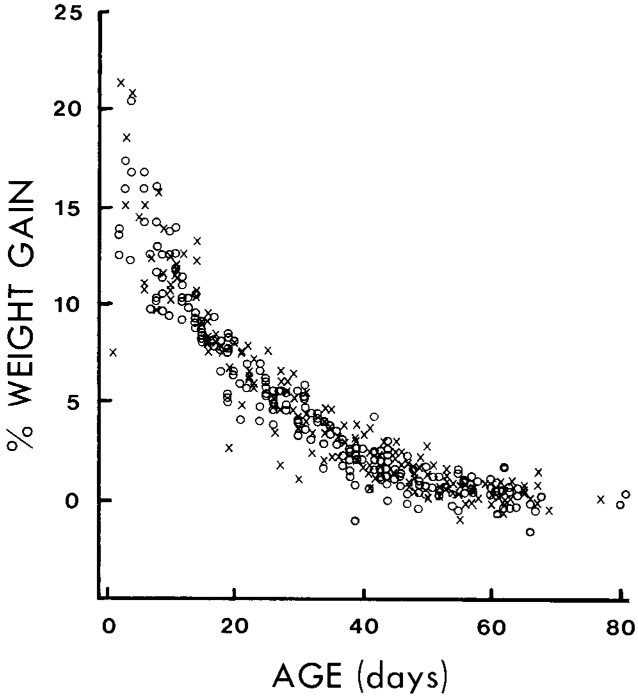

FIG. 3. Weight gain per day as a percent of body weight on that day, as a function of age for male (o), and female (x), nestling Bald Eagles. Each point represents a single measurement.

The volume of its egg (100.8 ml, calculated from the equation in Stickel et al. 1973) was only 86% of the mean volume (116.95 ml, SD = ±12.010, N = 18) for all other eggs I examined. However, as it is the relative size of the body components that is of interest in this paper, absolute size and sex of this eaglet are inconsequential.

The average value for the various body measurements per day of age for males and females is illustrated in Fig. 4. While the sexes were initially the same size, sexual dimorphism began to appear in some variables after 20 days of age (also see Bortolotti 1984a). As shown in Table 1, the parameters of the Gompertz equation for culmen length growth exhibited the same differences between the sexes as those of weight.

The relative growth of the body components is shown in Fig. 5. The length and width of the tarsus and length of the mid-toe reached asymptotic size at about the halfway point in the nestling period (Fig. 4). These three variables were characterized by a logistic growth curve. The hallux

TABLE 2
SIZE OF A BALD EAGLE NEAR HATCHING AGE

| Variable | Absolute size[a] | Relative size (% of asymptotic size)[b] |
|---|---|---|
| Bill depth[c] | 9.0 | 26 |
| Culmen length[d] | 10.7 | 21 |
| Tarsus width[d] | 2.9 | 19 |
| Tarsus length[d] | 9.1 | 13 |
| Mid-toe length[d] | 8.9 | 13 |
| Hallux claw length[c] | 4.1 | 10 |
| Foot pad length[d] | 16 | 6 |
| Weight[d] | 73[e] | 2 |

[a] Linear measurements in mm, weight in g.
[b] Mean size of the sexes.
[c] See Bortolotti (1984c) for asymptotic size.
[d] See Bortolotti (1984a) for asymptotic size.
[e] Estimate based on the relationship between egg volume and egg weight (Bortolotti, unpubl.).

claw, culmen length, and bill depth conformed to the Gompertz equation and were still growing when the birds left the nest.

*Flight feathers.*—When the length of the eighth primary was used in a linear regression as a predictor of age, the confidence limits about individual predictions were about ±3 days, with similar results for central rectrix length (Bortolotti 1984a). To test for sexual differences in development, I randomly selected a subset of data whereby males and females were represented by equal numbers of first-hatched (C1) and second-hatched (C2) nestlings to avoid any bias that hatching sequence may introduce. This data set was comprised of 78 measurements of males and 72 measurments of females for both eighth primary and central rectrix. The emergence of the eighth primary (i.e., the intercept of the regression equation) was significantly earlier for males than for females ($F = 15.84$, df = 1,147, $P < 0.0001$). The same pattern was true for the emergence of the central rectrix ($F = 18.07$, df = 1,147, $P < 0.0001$). There was no statistical difference (*P*s > 0.05) between the sexes in the slope of the regressions (i.e., the rate of growth) for either the primary feather or the rectrix.

For neither sex was the growth of flight feathers complete at the time of nest departure, as apparently is the case for several raptors (Brown and Amadon 1968). Young eagles frequently leave the nest before they can fly and have to spend a few days on the ground (pers. obs.). I captured 20 eaglets that had "prematurely" left the nest, and sheaths of growing flight feathers were evident on all of them. The asymptotic size of the flight features was not known. If, however, the lengths of the eighth pri-

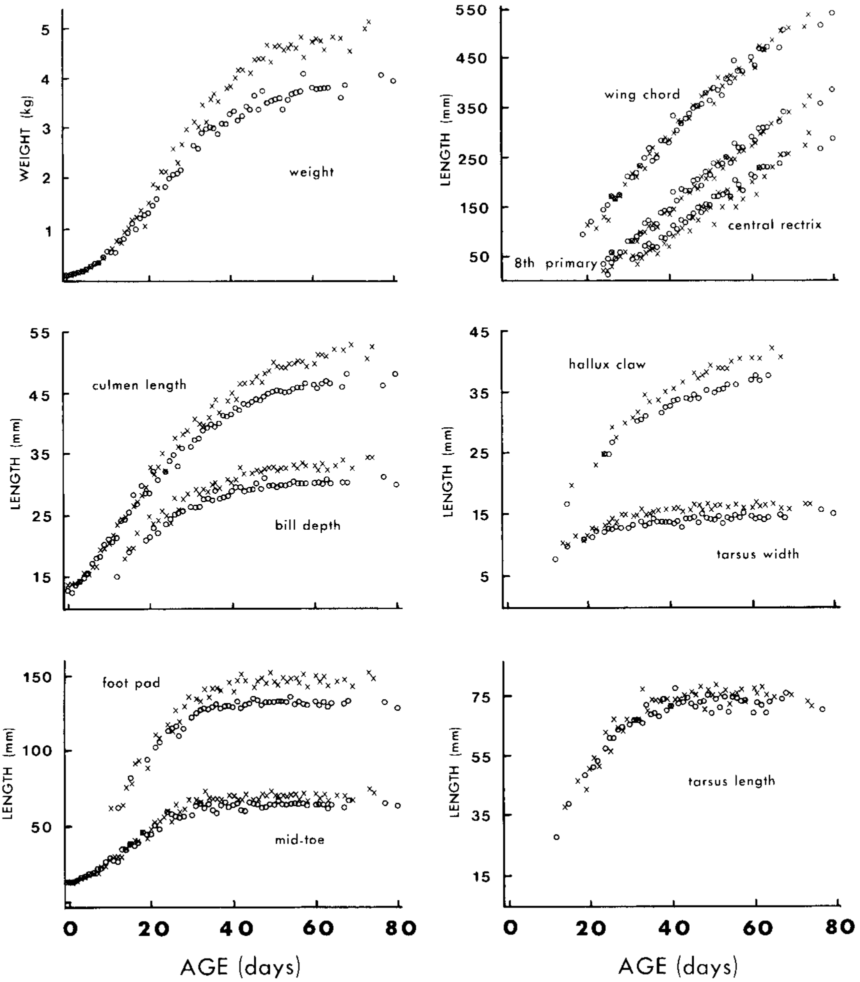

FIG. 4. Mean size as a function of age for body measurements of male (o), and female (x), nestling Bald Eagles.

mary, wing chord, and central rectrix of study skins (youngest plumage class of Bortolotti 1984c) are comparable to the asymptotes of these characters for nestlings, then measurements made on the captured birds reveal that only 80%, 88%, and 84%, respectively, of growth was completed. Eaglets on the ground were usually airborne within a day or two and it is unlikely that feather growth could have been completed in that time. Because flight feathers were not fully grown until after nest departure,

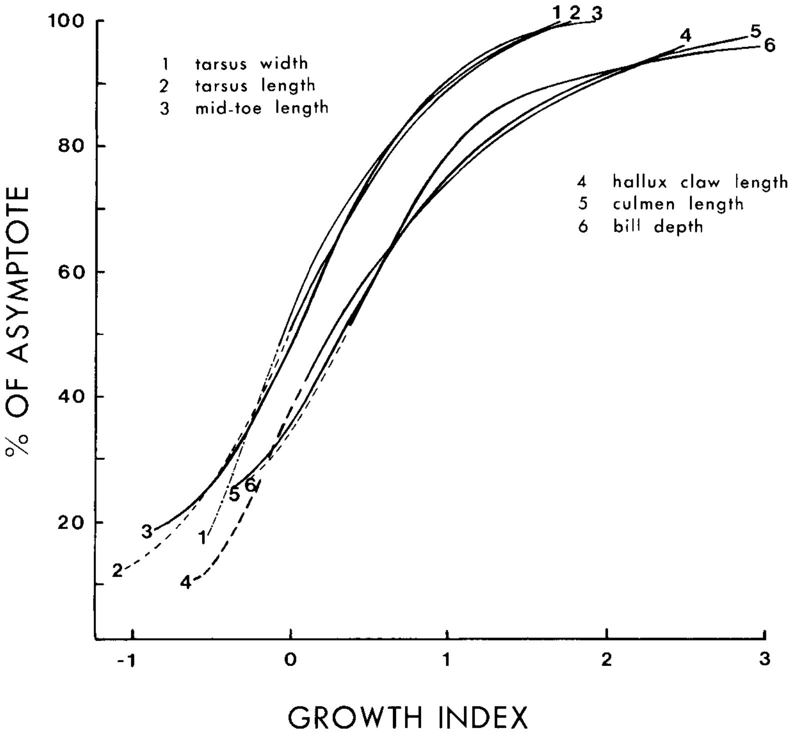

FIG. 5. The relative growth (percent of asymptote attained in relation to the growth index) for culmen length, bill depth, hallux claw length, mid-toe length, and the length and width of the tarsus (for females only, see text).

and because of the earlier feather development of males, sexual size dimorphism was not apparent in the measurements of wing chord, eighth primary, and central rectrix made during the nestling period (Fig. 4). The mature sizes of these variables are, however, significantly sexually dimorphic (Bortolotti 1984c).

To examine the potential effect that order in the hatching sequence may have had on flight feather growth, I compared C1s to C2s within each sex. For eighth primary length, the slopes of regressions were not statistically significantly different (*P*s $> 0.05$) for either sex, but the intercepts were significantly different for males ($F = 4.74$, df = 1,99, $P = 0.03$) and females ($F = 30.04$, df = 1,92, $P < 0.0001$). The rate of central rectrix growth also did not differ between chicks (*P*s $> 0.05$), but the timing of the intercept did for males ($F = 4.95$, df = 1,99, $P = 0.028$) and females

($F = 16.14$, df $= 1{,}92$, $P = 0.0001$). The emergence of both feathers was delayed for C2 compared to C1.

For a more detailed investigation of factors influencing flight feather growth, I calculated a linear regression equation for the relationship between age and the length of the eighth primary for each nestling for the linear period of feather growth (up to 72 days of age, Bortolotti 1984a). This allowed comparison of both the growth rate and time of emergence of the primaries to the weight growth parameters $K$ and $t$. The growth rate constants $K$ were not significantly correlated with the slopes of the eighth primary regressions ($P > 0.05$), but were correlated with the intercepts for males ($r = -0.518$, df $= 24$, $P < 0.01$) and females ($r = -0.457$, df $= 19$, $P < 0.05$). These results are consistent with those of the previous investigation of the relationship of primary feather growth to sex and order in the hatching sequence; the timing of emergence of the feather, but not growth rate, was important. The intercepts of the eighth primary regressions were also significantly correlated with the inflection points of the weight growth curves for males ($r = 0.655$, df $= 24$, $P < 0.01$) and females ($r = 0.607$, df $= 19$, $P < 0.01$).

*Body feathers.*—Fig. 6 shows the general appearance of nestlings of various ages. Upon hatching, eaglets were covered with a light beige-gray prepennae down (Fig. 6A). The color was more or less uniform over the body. Bent (1937) described the first down of the southern Bald Eagle (*H. l. leucocephalus*) as smoke-gray on the back, paler gray on the head and underparts, and nearly white on the throat.

The first down was gradually replaced by a noticeably darker medium gray second (preplumulae) down. The second down began to appear through the skin between 9 and 11 days of age (Fig. 6B). No sex difference was noted in the timing of the growth of the second down, but there was an effect for the order with which nestlings hatched within a nest. In broods of two chicks, emergence of second down of the second-hatched chick (C2) was delayed by about 1 day compared to the first-hatched chick (C1) (Sign test, $N = 9$, $P = 0.02$). The retarded development of C2 is evident in Fig. 6C. Although the siblings in Fig. 6C were only 1 day different in age, their plumage would suggest a greater disparity. By 18–22 days of age very little first down was visible on the body except for the top of the head, where second down was beginning to show (Fig. 6D).

The first contour feathers to show on the body were those of the humeral tract, appearing as dark epaulets (Fig. 6E). These first became evident on day 24–31. Feathers on the head and upper back first appeared on day 25 at the earliest and day 34 at the latest (Fig. 6F). Feathers on the lateral ventral surface became noticeable between day 26 and 45 (Fig. 6G), and

FIG. 6. Physical appearance of Bald Eagle nestlings of different ages (actual age and an approximate range of possible ages for a bird of that degree of development): (A) 2 days (1–5); (B) left = 8 days (6–9), right = 10 days (10–13); (C) left = 13 days (12–16), right = 12 (9–12); (D) 19 days (18–23); (E) left = 24 days (19–23), right = 26 days (24–31); (F) 28 days (27–35); (G) 44 days (32–48); (H) 56 days (50–65). The white card shown in some photographs was 7.6 × 12.7 cm in size.

those covering the tarsi were last to show between 39 and 55 days of age (Fig. 6H).

There was no indication of a sex difference in the timing of appearance of body feathers. However, this would have been very difficult to detect given the large variance associated with the age of appearance of feathers for most parts of the body, particularly those developing late in the nestling period. Collopy (1980) found no difference in the rate of development of six of eight feather tracts of nestling Golden Eagles (*Aquila chrysaetos*). According to Newton (1978), male Sparrowhawks (*Accipiter nisus*) appeared to have more advanced plumage than females.

It was strikingly obvious to me in the field that two eaglets of the same age could look very different because of the variability in timing of emergence of body feathers. To investigate the degree to which differences in body feather maturation were correlated with other developmental processes, I classified the birds as being either early or late. The criteria for early developers were: the age of appearance of feathers had to be less than or equal to 26 for the humeral tract, 30 for head and back feathers, and 43 for tarsal feathers. My field notes were detailed enough to determine the timing of feather growth for 19 early and 14 late developers. I used Mann-Whitney *U*-tests to compare early and late classes. There were no significant differences ($P$s $> 0.05$) for $K$s (sexes combined), $t$s (sexes tested separately), and $a$s (sexes tested separately) of the weight growth curves. The slopes of the individual eighth primary regressions were not different between groups ($P > 0.05$). There was also no difference for eighth primary intecepts for males ($P > 0.05$), but there was a significant difference for females ($P < 0.01$). Although there was little or no association between body feather development and weight and primary feather growth, the early and late categories do seem to be good indicators of development; there was a significant difference in the age at which males ($P < 0.01$) and females ($P < 0.01$) departed from the nest. Early developing males left an average of 4.8 days younger than late developing males. Early developing females left an average of 4.7 days younger than late developing females.

*Homeothermy.*—I did not empirically determine the age at which nestlings began to thermoregulate. Dunn (1975) found that growth rate ($K$) was a good predictor of the age at which altricial birds became homeothermic. If Bald Eagles are comparable to the species Dunn (1975) examined, then eaglets should have begun to thermoregulate at 14.7 days of age ($K$ was first converted to the logistic equation equivalent [Ricklefs 1973]). If the interspecific relationship of $K$ and age of homeothermy derived by Dunn (1975) also applies intraspecifically, then the range of

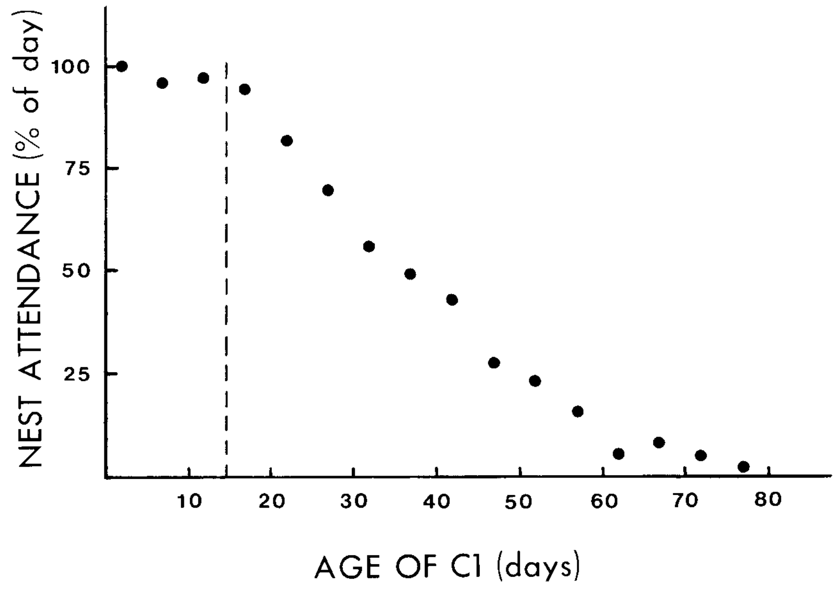

FIG. 7. Percent of time at least one adult Bald Eagle was in attendance at the nest as a function of the age of the first-hatched chick (C1). Points represent the mean for 5-day periods, plotted mid-way into each period. The dashed line marks the estimated age at which eaglets began to thermoregulate.

ages for eaglets was 14.5–15.1 days. Most species of altricial birds brood their offspring for a large portion of the day until the chicks begin to thermoregulate. As the ability of the nestlings to control their own temperature improves, the adults should be free to spend increasing amounts of time away from the nest foraging (Dunn 1975). This may be true for Bald Eagles, for the estimated age of homeothermy coincides with a sharp decline in the amount of time at least one adult is present at the nest (Fig. 7).

## DISCUSSION

*Feather development.*—Little is known about the functional significance and implications of different patterns of feather growth (Ricklefs 1983). The development of Bald Eagles is typical of other falconiforms; wing and tail quills are first to emerge, and then the body feathers with those on the upper side being earliest (Brown and Amadon 1968).

Plumage development is associated with the acquisition of homeothermy (Ricklefs 1983). At the time when eaglets were estimated to become homeothermic, feather development was restricted to an increase in the proportion of second down. The second down is much thicker than the first (Herrick 1932, Bent 1937, pers. obs.), and thus presumably has better insulative properties. Given that the emergence of second down is delayed in C2 eaglets, C1 nestlings may be able to achieve "effective," if not "physiological" (see Dunn 1975), thermoregulation at a younger age than C2s.

Hatching order within a brood also had an effect on the timing of emergence of the eighth primary and central rectrix. Although not quantified in this study, body contour feather development appeared to be delayed as well. Examples of how much the feather development of C2 chicks can be hindered by the presence of an older sibling can be seen in photographs of White-tailed Eagles (*H. albicilla*) in Mori (1980), and of Booted Eagles (*Hieraaetus pennatus*) in Steyn (1983). A comparison of the appearance of the siblings in these two examples would suggest an age disparity between them far in excess of the actual difference. Undoubtedly, the same phenomenon led Broley (1947) to believe that Bald Eagle eggs could be laid 2–3 weeks apart because of the apparent age difference of chicks within a nest (eggs usually hatch 1–3 days apart [Bortolotti 1984b]).

The development of body feathers was not associated with any parameters of the weight growth curves. This is likely because most of the body feathers began to emerge relatively late in the nestling period. Eaglets reached approximately 45% of asymptotic weight when the first contour feathers appeared, and 75% when the legs began to feather out. Feather growth may have been influenced by short-term effects, e.g., a variable food supply, that were of little consequence to weight gain at that particular stage of development. Body feather growth also appeared to be independent of growth rate of the eighth primary and perhaps its timing of emergence as well.

Unlike body feathers, aspects of eighth primary growth were associated with weight growth parameters. The appearance of the feather was significantly correlated with $K$ and $t$ of the weight growth curves. The eighth primary emerged from the wing at about the time of maximum weight gain (i.e., the inflection point of the weight growth curve) and thus both weight and feather growth may have been influenced by the same environmental and physiological conditions. I did not find any significant relationships to explain the variation in the rate of eighth primary growth. Ricklefs (1984) found that the more rapid the weight growth of European Starlings (*Sturnus vulgaris*), the earlier the primary feathers began to grow, but the rate of feather elongation was not affected. Several researchers studying raptors have found that flight feathers show relatively little variance in growth rate and are less likely to be influenced by food shortages than weight growth (Scharf and Balfour 1971, Moss 1979, Picozzi 1980, Olsen et al. 1982). In contrast, Zach and Mayoh (1982) found that the flight feather growth of Tree Swallows (*Tachycineta bicolor*) was more variable than weight growth. While the appearance of the feathers of swallows with long nestlings periods was delayed, there was no relationship between the timing of feather growth and weight growth.

Flight feather growth varies little among individuals compared to body feather development. This suggests a high priority of functional importance for flight feathers (O'Connor 1977). The relative independence of body and flight feather growth may allow for energy and nutrients to be restricted to areas of relatively great importance to post-fledging survival. If this is true, the detriment of food shortages to the growing young is minimized. This is not to say that body feather development is unimportant, for it may be indicative of other developmental processes of the body. This is suggested by the fact that "early" birds left the nest nearly 5 days sooner that "late" birds. Body feather development may thus be a useful means of monitoring environmental stress in this species.

*Body size.*—Interspecifically, growth rate is inversely related to body size in birds (Ricklefs 1968). Such is not the case intraspecifically; rapid growth of eaglets was associated with early inflection points of growth curves, but neither of these attributes were related to the asymptotic weight. The Bald Eagle grows at a rate expected of an altricial bird of its size. Ricklefs' (1968) model of growth rate and body weight for temperate zone passerines and raptors predicts a rate (using $t_{10-90}$, an inverse measure of growth) of 41.2 days, whereas the observed was 45.1. Because eagles are large and have a semi-altricial mode of development, absolute growth rate should be substantial. In fact, the Bald Eagle may gain more weight per day than any other North American bird. I have not found any reference to species exceeding the maximum weight gain of 180 g/day (a conservative figure, see Results) reported here.

Several hypotheses have been proposed to account for species-characteristic growth rates in birds. They are reviewed in Ricklefs (1983) and tested for eagles in Bortolotti (1984b) and so will not be discussed in detail here. I will, however, comment on the relevance of data presented here to aspects of the topic.

Ricklefs (1973, 1979a, 1979b) proposed that the rate of growth of any body component is constrained by a compromise between allocation of tissue to embryonic and mature functions. The more mature the tissue is, the slower its growth rate will be. Consistent with this hypothesis is the slow growth of the Bald Eagle's bill. The bill is not only functional in feeding, as eaglets must initially take food from their parents' bills (they do not gape) and then later tear up prey themselves, but it is also important in sibling conflicts. Very young eaglets are capable of forceful bites and pecks, and of shaking a sibling from side to side. Eaglets also begin preening soon after hatching, which may be important in reducing parasite loads (Bortolotti 1985). Of course, the bill is not the only body component associated with performing these behaviors, and perhaps the maturation of jaw muscles is the more important consideration. Seemingly inconsistent with the tissue-allocation hypothesis is the slow growth of the hallux claw which has a low degree of functional maturity in the nestling period. Perhaps the growth of the bill and claw are slow partly because of their horny exteriors. The hard sheath covering the bone may not be capable of more rapid elongation and thus limits growth.

A comparison of growth rates of various parts of the body, within and among species, led Ricklefs (1979a) to believe that the overall growth rate of an individual was limited by the most slowly growing component. The slow growth of the bill (and presumably head) probably does not limit the overall rate to any great degree because a large proportion of bill growth was achieved prenatally (Table 2), thus allowing for faster growth postnatally (Ricklefs 1979a).

## CONCLUSIONS

It is tempting to hypothesize scenarios of adaptive significance to explain variation in growth rates (O'Connor 1977, 1978; Werschkul 1979). However, it is difficult, if not impossible in most cases, to attribute the patterns of growth directly to natural selection acting on growth itself. Alternative explanations are possible such that the observed growth rate is merely the consequence of selection operating on other factors (Ricklefs 1983).

Several studies of the growth of birds that are sexually dimorphic in size have documented a similar pattern of development of the sexes (see review by Richter 1983). The smaller sex is characterized by earlier development of feathers, faster attainment of asymptotic size, and earlier flights from the nest. That this is true regardless of whether males or females are the larger sex suggests that biochemical processes in growth likely proceed at a specific rate and sex-related differences are the allometric consequence of size dimorphism. When the difference in size is accounted for, males and females grow at the same rate (Fig. 1). While sexual dimorphism in growth dynamics may have several important consequences for nestling survival (Newton 1978, Bortolotti 1984b), and sex ratio (Richter 1983, Bortolotti 1984b), the rate of growth is unlikely to have been the primary adaptation in such cases.

Results of this study consistently showed that the timing of growth events, whether in regard to sex differences or the effect of hatching sequence, was a more important consideration than rate of growth in assessing development. Growth studies have traditionally lacked emphasis on the timing of growth events compared to the concern for the rate at which growth proceeds. This may be in part because of the mathematical ease of comparing $K$ values among species characterized by different growth equations (Ricklefs 1968, 1973). Studies of intraspecific variation are not so limited, and researchers should strive to document as many facets of growth as possible.

## SUMMARY

Developmental changes in color, weight, body size, and the appearance of body contour feathers, are described for wild nestling Bald Eagles (*Haliaeetus leucocephalus*) in Saskatchewan. Chicks hatched with relatively large bills, large legs, and a small body. The growth of some body components (e.g., the legs) was complete about halfway through the nestling period, whereas the mature size of the bill and flight feathers was not reached until after the birds left the nest. The maximum absolute weight gain per day (180 g, a conservative figure) of Bald Eagles appears to be the greatest of any North American bird, but this is to be expected of a temperate zone altricial species of its body size. Weight growth was not correlated with body feather development or the rate of eighth primary feather growth, but was significantly correlated with the timing of the emergence of the eighth primary. There was a great deal of variation in the age at which body feathers unsheathed, yet little variation in the growth of flight feathers. Body feather growth and primary feather growth were largely independent. Males differed from females in being smaller, having earlier inflection points to growth curves and growing flight feathers at a younger age, but were not different in rate of growth. When body size was accounted for, the relative growth of the sexes was equal. The emergence of second down and flight feathers was delayed for the second-hatched chick in the nest compared to its older sibling. The age at which eaglets became homeothermic was estimated to be about 15 days, at which time a sharp decline in the nest attentiveness behavior of the parents was observed. Caution must be exercised when attempting to determine the adaptive significance of patterns of growth, for growth itself may not have been the primary adaptation. Several analyses presented here showed that the timing of growth events, rather than the rate at which they proceed, was the more important consideration in assessing development.

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DEPT. ZOOLOGY, UNIV. TORONTO, TORONTO, ONTARIO M5S 1A1 CANADA. ACCEPTED 25 SEPT. 1984.

## CHANGE IN EDITOR

**Dr. Keith L. Bildstein** will be serving as the Editor of The Wilson Bulletin beginning with Volume 97. As of 15 May 1984, all manuscripts submitted for publication in the journal should be sent to him at the **Department of Biology, Winthrop College, Rock Hill, SC 29733.** All manuscripts received prior to 15 May 1984 will continue to be processed by Dr. Jon C. Barlow.