Evolution of Growth Rates in Eagles: Sibling Competition Vs. Energy Considerations

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EVOLUTION OF GROWTH RATES IN EAGLES:
SIBLING COMPETITION VS. ENERGY CONSIDERATIONS[1]

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Abstract. Nestlings of birds that raise only one young (B1 species) grow slower than those of birds that raise more than one young (B2 species). B2 species may be fast growing because sibling competition exerts a strong selective force for rapid growth. Other hypotheses have been proposed to explain the slow growth of B1's. To overcome the problem inherent in previous investigations of comparing species widely divergent in ecology and phylogeny, I analyzed patterns of variation in growth of one group only: eagles of the world. I fitted growth curves to data obtained from the literature for some species, but most eagles were compared using the length of the nestling period as an indicator of growth rate. I also collected data on the growth of wild Bald Eagle (*Haliaeetus leucocephalus*) nestlings. I investigated how postnatal growth may be related to brood size, clutch size, nestling mortality, body size, and prenatal growth. B1 eagles were found to grow slower than B2 eagles. Differences in foraging ecology, diet, and mode of development are unlikely to account for the observed variability in the rate and form of growth. Contrary to the sibling competition hypothesis, growth rate was not correlated with the intensity of sibling competition. Eagles that regularly lay two eggs but always lose one chick because of sibling competition (obligate fratricide) grow slower than those species in which such mortality may or may not occur (facultative fratricide). Species characterized by facultative fratricide grow at a rate expected for their adult body size, whereas B1 species do not. B1 eagles are characterized by growth curves with early inflection points compared to B2 eagles. The shape of the growth curves and slower growth rates of B1 species are contrary to predictions of the sibling competition hypothesis, and may instead have resulted from selection to reduce peak energy requirements of the nestlings. I present a model of the effect of hatching interval, species-specific growth rate, and relative growth of siblings, on the probability of fratricide, which suggests that sibling competition is not an important factor in selecting for rapid growth.

Key words: Accipitridae; avian growth; eagles; food limitations; fratricide; sibling competition.

INTRODUCTION

Avian growth rates have been the subject of several extensive reviews (Lack 1968, Ricklefs 1968a, 1973, 1983, Case 1978, O'Connor 1978a, Drent and Daan 1980). It appears that much of the variation in growth rate among species can be explained by adult body size and mode of development (i.e., precocial vs. altricial) (Ricklefs 1968a, 1973). There also exists, however, a clear relationship between brood size and nestling growth rate, although its evolutionary significance has been the subject of much debate. Ricklefs (1968a) found that nestlings of birds laying only one egg grow slower than those of birds that laid more than one, and suggested that food limitations may have led to a reduction in growth rate of species in the former group. Werschkul and Jackson (1979) investigated this further for numerous taxa and proposed that sibling competition was a major force selecting for rapid growth. Implicit in the latter hypothesis is the argument that genetic difference in growth among siblings may result in differential mortality within a brood. In his re-examination of the growth/brood-size relationship, Ricklefs (1982) questioned Werschkul and Jackson's sibling competition hypothesis and suggested that the growth of species raising only one chick may be limited by the

quality or quantity of food or that differences between slow- and fast-growing species may only reflect differences in ecology or mode of development. Testing the sibling competition and alternative hypotheses has been problematical since mutually exclusive predictions have not been formulated given the taxonomic and ecological diversity of species examined. To resolve this problem I have analyzed patterns of growth in eagles (Falconiformes: Accipitridae).

Eagles are particularly appropriate subjects to test hypotheses concerned with the relationship between brood size and growth rate. Brood size is invariably one in some species (B1), and from one to three in others (B2) (see Methods); sibling competition (fratricide) is a significant source of nestling mortality (Brown 1976). Unlike most birds, different degrees of sibling competition can be compared among eagles, because fratricide is characteristically either obligate (a chick is always killed by its sibling) or facultative (mortality may or may not occur) for each species (Edwards and Collopy 1983, Mock 1984a) (Fig. 1). It is not my intention to discuss all aspects of brood reduction (see Mock 1984a for a review). Instead, I question whether or not within-brood nestling mortality attributable to differential growth among siblings has been a significant influence on the evolution of avian growth. The similarities among eagles with respect to overall morphology, relative freedom from nest predation, and breeding biology, alleviate some of the confounding factors in previous comparative studies of avian growth

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and nestling mortality. Eagles are a group arbitrarily defined on the basis of morphology and general ecology (i.e., they are large predatory birds), yet they are similar enough taxonomically to allow for meaningful comparisons to be made among species. Because eagles are highly variable in their food habits, body size (a 10-fold range in mass), and habitat preference, hypotheses concerned with the energetic consequences of brood size and growth rate (Ricklefs 1982) can also be tested (Fig. 1). In this paper I examine how postnatal growth of eagles may be related to brood size, clutch size, nestling mortality, body size, and prenatal growth, to distinguish between alternative hypotheses. Using data on Bald Eagles (*Haliaeetus leucocephalus*), I present a model of the effect of hatching interval, species-specific growth rate, and relative growth of siblings, on the probability of fratricide, to investigate the potential of sibling competition as a selective force influencing growth.

METHODS

I studied the growth and behavior of nestling Bald Eagles over the entire nestling periods from 1980–1982 on Besnard Lake, Saskatchewan (55°20′ N, 106°00′ W). The lake supports about 25 pairs of breeding Bald Eagles, and many aspects of this population's biology have been described (e.g., Gerrard et al. 1975, 1978, 1983). I observed the behavior of two-chick broods and their parents from nearby tree-top (Bortolotti 1982) or ground blinds at two nests in 1980, and three nests in both 1981 and 1982. I took detailed behavioral notes for a total of 1025 h over 137 d, approximately evenly distributed among nests and over the entire nestling period. I documented clutch size, hatching interval, and nestling growth and survival by repeatedly climbing to nests. Using the graphical technique of Ricklefs (1967), I fitted individual Gompertz growth equations to 20 male and 18 female eaglets of known age from 19 nests. The parameters K (a constant proportional to the overall growth rate) and t (the inflection point) were determined from the graph for each bird, and a (the asymptotic mass) was estimated as part of the methodology. Detailed accounts of methods and nestling development are presented in Bortolotti (1984a, b, c). "Growth" is intended to mean the ontogenic increase in mass.

I also fitted logistic, Gompertz, and von Bertalanffy growth curves, where appropriate, to eight other species of eagles for which raw data were available in the literature (nomenclature follows Brown and Amadon 1968): Crowned Eagle *Stephanoaetus coronatus* (Tuer and Tuer 1974), Long-crested Eagle *Lophaetus occipitalis* (Steyn 1978), Black (Verreaux's) Eagle *Aquila verreauxi* (Gargett 1970, 1972), Tawny Eagle *A. rapax rapax* (Steyn 1973), White-tailed Eagle *Haliaeetus albicilla* (Mori 1980), and from Brown et al. (1982) the Brown Snake Eagle *Circaetus cinereus,* Bateleur *Terathopius ecaudatus,* and African Hawk-eagle *Hieraaetus fasciatus spilogaster.* Some caution must be exer-
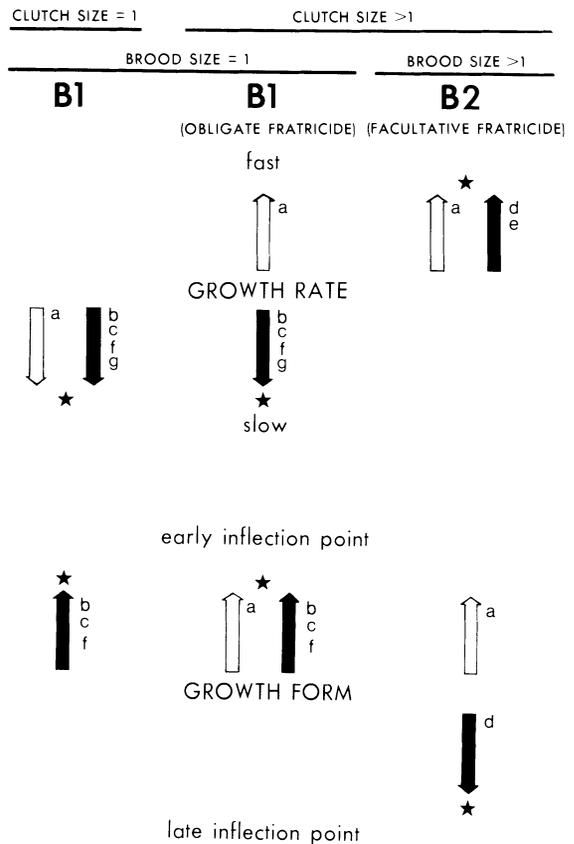

FIG. 1. A comparison of the predictions and rationale of the sibling competition (open arrows) and alternative (solid arrows) hypotheses to account for differences in growth rate and form of the growth curve between species raising one young (B1, by laying one egg or through obligate fratricide) and species raising more than one young (B2). Letters beside arrows refer to possible reasons for the directions indicated: (a) sibling competition, (b) to reduce energy requirements, (c) high nestling mortality dependent on brood size, (d) high nestling mortality independent of brood size, (e) resource levels do not limit growth, (f) resources are limited, (g) nutrients are limited. Stars show the direction supported by data for eagles.

cised here since most studies reported only one or a few birds and there can be intraspecific variation. Data on growth curves were available for a large sample of Golden Eagles (*A. chrysaetos*) from Collopy (1980). I also calculated the variable t_{10-90} from the growth equation for each species. This is an inverse measure of growth rate, representing the time taken to grow from 10 to 90% of the asymptotic mass, and so largely encompasses the linear portion of the growth curves. As this section of the curve is similar for all three growth equations, the growth of species fitted to different types of curves can be compared without conversion.

Because growth data do not exist for most species of eagles, I used the length of the nestling period (i.e., fledging age) as an indicator of relative growth rate (Ricklefs 1968a). I primarily used the data on clutch and brood sizes and the lengths of the incubation and nestling periods provided by Brown (1976:211), but

TABLE 1. Growth parameters of species of eagles raising one young (B1) and more than one young (B2).

Brood size	Species	Growth equation*	K_G†	t_{10-90} (d)	t‡ (d)	a (g)
B1	Crowned Eagle‖	von Bertalanffy	0.024	101.6	28.3	2950
	Black Eagle‖	Gompertz	0.064	48.1	22.8	3510
	Tawny Eagle‖	Gompertz	0.063	49.0	19.6	2600
	Bateleur¶	Gompertz	0.044	70.1	26.6	2100
	Brown Snake Eagle¶	von Bertalanffy	0.025	98.0	23.4	2100
B2	Bald Eagle§	Gompertz	0.068	45.1	21.3	4629
	White-tailed Eagle	Gompertz	0.070	44.1	19.4	4250
	Golden Eagle§	Logistic	0.086	34.8	25.0	3518
	Long-crested Eagle	Logistic	0.089	33.5	23.7	1350
	African Hawk-eagle	Logistic	0.105	28.5	19.0	1200

* Gompertz equation: $m = ae^{-be^{-kt}}$; logistic equation: $m = a(1 + be^{-kt})^{-1}$; von Bertalanffy: $m = a(1 - be^{-kt})^3$, where m is the mass of the growing bird, a is the asymptote (final mass), e is the base of natural logarithms, k is a constant proportional to the overall growth rate, and b is a constant translating the time axis such that time t is equal to zero at the inflection point ($b = \frac{1}{3}$ for the von Bertalanffy equation and $b = 1$ for both the Gompertz and logistic equations).
† For logistic and von Bertalanffy equations, K's have been converted to the Gompertz form for direct comparison among species.
‡ t (inflection point) has not been converted to a common growth form.
§ Average for the sexes.
‖ Obligate fratricide species.
¶ Species lays only one egg.

made corrections if more recent literature suggested the need for changes. In addition to the species listed by Brown (1976), data were also available for the Harpy Eagle *Harpia harpyja* (Rettig 1978), Grey-headed Fishing Eagle *Ichthyophaga ichthyaetus* (Ali and Ripley 1968), Steller's Sea Eagle *Haliaeetus pelagicus* (Brown and Amadon 1968) and the Lammergeier *Gypaetus barbatus* (Brown and Amadon 1968, Cramp 1980). The latter species is an Old World vulture (Accipitridae) similar to eagles in some behaviors (Brown and Amadon 1968), and is included here because it is obligately fratricidal and is thus a valuable comparison to other species. The mean mass of the sexes was used as a measure of body size (data primarily from Brown and Amadon 1968).

Edwards and Collopy (1983) identified the Crowned, Black, and Lesser Spotted (*A. pomarina*) eagles as species characterized by obligate fratricide. I also consider Ayre's Hawk-eagle (*Hieraaetus dubius*) to be obligately fratricidal (see Brown 1976), although its usual clutch appears to be one egg. I also treat the Tawny Eagle as a species for which fratricide is obligate, for although two chicks are occasionally reared (Osborne 1982), fratricidal behavior is as extreme as that observed in Black Eagles (Gargett 1978) and usually only one chick survives (Steyn 1973, Cramp 1980, Brown et al. 1982). A species that typically raises only one young, either as a result of obligate fratricide or the laying of one egg, will be referred to as a B1 species. Eagles that frequently raise more than one young will be referred to as B2 species.

RESULTS AND DISCUSSION

Variation in growth rate

Table 1 summarizes growth parameters for the 10 species fitted to growth curves. K's converted to the Gompertz form of curve are presented to allow direct comparison among species (see Ricklefs 1973, Werschkul and Jackson 1979). To compare species for which growth curves could not be fitted, the age at fledging was plotted against the mean asymptotic mass of the sexes (Fig. 2). The assumption that fledging age is an indicator of growth rate (Ricklefs 1968a) proved to be valid, as the two are strongly correlated for the species in Table 1 ($r = 0.878$, df = 8, $P < .01$). The results in Fig. 2 compare well with the findings of both Werschkul and Jackson (1979) and Ricklefs (1982), in that B1 species grow slower than B2 species ($F = 16.86$, df = 1,29, $P < .001$). A distinction is made in Fig. 2 between temperate and tropical species because Brown (1976) believed that the latter are characterized by longer development periods. The association between brood size and growth rate, however, is stronger than that between latitudinal or geographic distribution and growth rate. Although almost all B1's are found in the tropics and grow slowly; nearly 30% of B2's are tropical species, yet grow relatively quickly (Fig. 2).

The number of species considered in this study could have been increased if other falconiformes were included. However, I chose to limit the study to species with small clutches, thereby excluding smaller raptors. In other cases, including several eagles, data were not available. For example, the breeding biology of the large Old World vultures is poorly documented, but almost all lay one egg and have very long development periods, as would be predicted by the B1 regression. For example, the White-backed Vulture (*Gyps africanus*), Cape Vulture (*G. coprotheres*), and Lappet-faced Vulture (*Torgos tracheliotus*), all weigh $\approx 5000-7000$ g (Brown and Amadon 1968) and have nestling periods of 125 d or more (Steyn 1983). The Secretary Bird (*Sagittarius serpentarius*: Sagittariidae) is a facultatively fratricidal bird of prey that weighs ≈ 3600 g, and
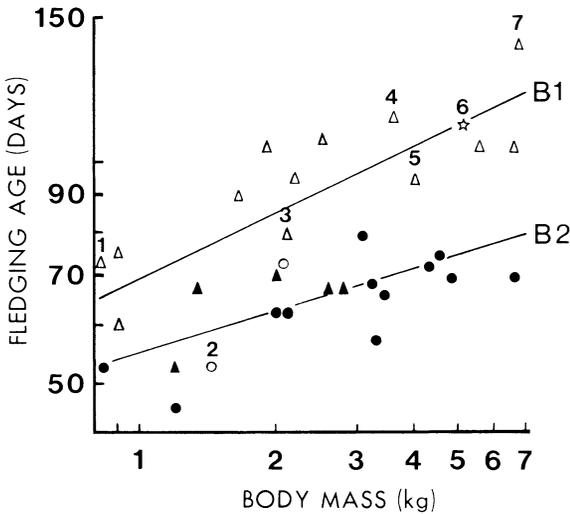
FIG. 2. Fledging age as a function of adult body mass for temperate (circles) and tropical (triangles) eagles with a brood size of 1 (open symbols) and >1 (solid symbols), and the Lammergeier vulture (star). Species that may lay two eggs but that rear only one young are numbered above their symbols: (1) Ayre's Hawk-eagle, (2) Lesser Spotted Eagle, (3) Tawny Eagle, (4) Crowned Eagle, (5) Black Eagle, (6) Lammergeier, (7) Harpy Eagle.

in common with other B2 species, its young fledge at ≈73 d old (Brown and Amadon 1968).

Ricklefs (1968a) analyzed data on clutch size and nestling period for nine species of eagles and found that those with clutches of one grew slower than those with clutches of two or more. He believed that the Ayre's Hawk-eagle and Wahlberg's Eagle (*A. wahlbergii*, point nearest to the Ayre's Hawk-eagle in Fig. 2) were exceptions because they laid one egg, yet grew relatively fast. However, they are not exceptions, for both species are small (<1000 g) and thus should be growing relatively faster than the larger species to which they were compared. Because species characterized by obligate fratricide have nestling periods as long as those laying one egg (Fig. 2), slow growth is correlated with brood size, not clutch size. This is further illustrated by the very slow-growing Harpy Eagle (the largest species in Fig. 2), which lays two eggs but stops incubating the second egg once the first has hatched (Rettig 1978). The single notable exception to the pattern of slow growth in B1 species is the Lesser Spotted Eagle, which has a short nestling period but raises only one young. Perhaps the fact that the Lesser Spotted Eagle migrates farther than all other eagles influences the duration of the nestling period. The fledglings apparently migrate alone from Europe to southern Africa only 1 mo after leaving the nest (Brown and Amadon 1968, Cramp 1980), and so development must be rapid. There is no other apparent association between the degree of migratory movement and growth rate.

The data strongly suggest that brood size is the overriding factor correlated with rate of development. The

relative growth of B1 and B2 species has been viewed from very different perspectives. Werschkul and Jackson (1979) believed that sibling competition promoted rapid growth in B2 species. Conversely, Ricklefs (1982) sought explanations for the slow growth of B1 species. Ricklefs (1968a, 1973) had previously found that much of the variation in avian growth rates could be explained by body size. The growth rate of B1 and B2 eagles (Table 1), in relation to body mass, is illustrated in Fig. 3. The line drawn in Fig. 3 was derived by Ricklefs (1968a) to describe the variation he observed in temperate zone passerines and raptors. The fact that B2 species lie remarkably close to this line implies that B2 eagles grow at a rate expected for their body size compared to other altricial birds, and that B1 species grow slower than predicted. The B1 species may not be strictly comparable to the passerine-raptor model because all are of tropical origin. However, two B2 eagles in Fig. 3 (including the near perfect fit) are tropical species. Given the trends in Figs. 2 and 3, B1 species are likely relatively slow growing for their size.

Ricklefs (1982) argued that because all of Werschkul and Jackson's (1979), and most of his own, sample of B1 species were pelagic seabirds, ecological or demographic factors unique to that group may have been responsible for the observed patterns. Several authors have remarked on the correlation between patterns of growth in seabirds and characteristics of their feeding ecologies; e.g., pelagic foragers are slow growing compared to inshore foragers (Lack 1968, Drent and Daan 1980, Ricklefs 1982). However, the differences observed among seabirds might also be related to the amount of energy brought to the chicks, the nutritional quality of the food, or to differences in precocity of development (Prince and Ricketts 1981, Ricklefs and White 1981, Ricklefs 1984a). Eagles cannot be placed into broad ecological groups comparable to the inshore-offshore distinction for seabirds. There is a great deal of variation in feeding habits within each brood-
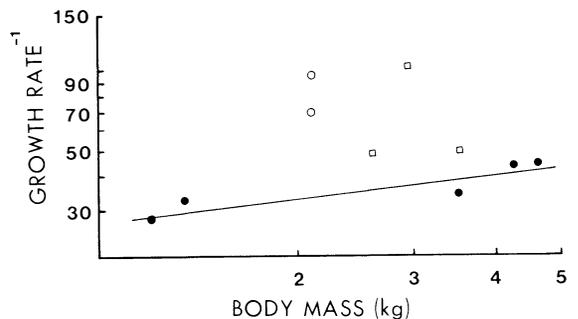

FIG. 3. An inverse measure of growth rate (t_{10-90}, the time taken to grow from 10 to 90% of adult body mass) as a function of adult body mass for species with a brood size of one (open symbols; O species laying one egg, □ obligately fratricidal species), and greater than one (●). Species are listed in Table 1. The line represents the relationship Ricklefs (1968a) found for temperate passerines and raptors combined.
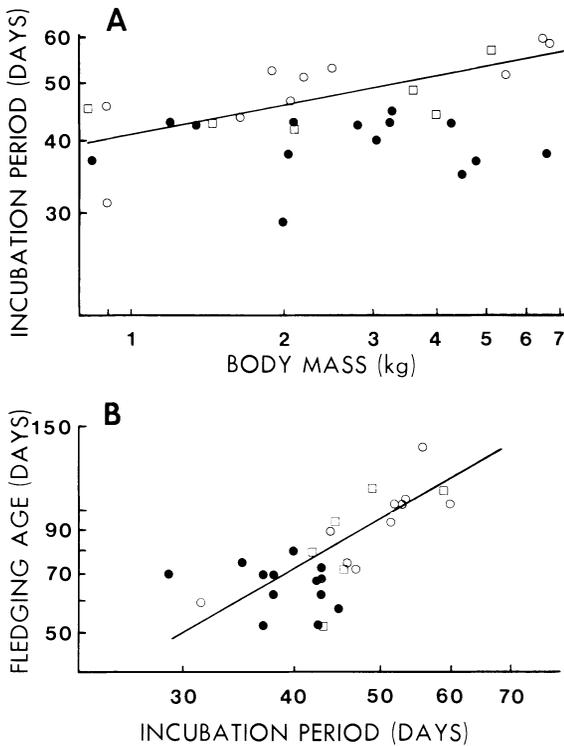
FIG. 4. (A) Adult body mass vs. length of the incubation period for eagles; line represents the significant ($P < .01$) relationship for species raising only a single young (B1 species). (B) Length of the incubation period vs. fledging age for eagles; line represents the significant ($P < .01$) relationship for species raising only a single young. [B1 species are open symbols (□ obligately fratricidal species, O species laying one egg), B2 species are solid circles.]

size group of eagles, and very often within each species. For example, B1's include the obligately fratricidal Crowned Eagle, which is capable of killing prey much larger than itself (Brown 1976), the Lammergeier, which feeds on bone marrow and other carrion (Brown and Amadon 1968), and the Tawny Eagle, which kills mammals and birds, pirates food from other birds, and regularly feeds on carrion and termites (Brown 1976). There does not appear to be a common ecological or physical trait among B1 species to account for their slow growth. The hypothesis that a nutritional deficiency may be responsible for the slow growth of B1's (Ricklefs 1983) also seems unlikely given the variability in food habits. Furthermore, and again unlike seabirds, there is no evidence to suggest that any eagle is more precocial at hatching than another. Therefore, it appears that qualitative differences in general foraging ecology, nutrition in the diet, and mode of development cannot be used to explain variability in growth rates among eagles.

Growth rate and nestling mortality

Raptor nestlings that die from either obligate or facultative fratricide do so almost invariably early in the nestling period (Steyn 1973, Meyburg 1977, Thaler and Pechlaner 1980, Edwards and Collopy 1983). At the time of sibling conflicts food is often abundant in the nest (Brown et al. 1977, Stinson 1979). Rather than competing for proximate resources, fratricidal siblings are ultimately competing for the position of sole survivor in the nest. According to the sibling competition hypothesis, natural selection favors rapid growth, as it gives a chick a competitive advantage over its nestmate(s). Growth rate should therefore be positively correlated with the intensity of sibling competition. This is not true for eagles, because species for which fratricide is obligate (i.e., where sibling competition is most intense) have slow growth similar to eagles laying only one egg (i.e., where there is no sibling competition) (Fig. 2). The sibling competition hypothesis' prediction that obligately fratricidal species should grow faster than facultatively fratricidal species is also not supported by the data (Fig. 2, Table 1), and in fact the opposite is true.

There are several possible causes of nestling mortality exclusive of fratricide. When mortality independent of brood size (e.g., bad weather, accidents) is greater than mortality dependent on brood size (e.g., starvation), selection should favor fast growth to shorten the nestling period (O'Connor 1978b). In some species where fratricide is facultative, such as the Golden Eagle (Kochert 1972) and the Bald Eagle (G. R. Bortolotti, *personal observation*), most nestling mortality is independent of brood size. If the B1 species are energy limited (Ricklefs 1982), then starvation would assume a more significant role than it likely would for B2 species, and thus selection would favor prolonged development. O'Connor (1978b) believed that growth variation as a means of adjusting the energy requirements of a brood to a limited food supply was plausible only when predation was negligible. Very low rates of predation on eaglets are likely characteristic of most species of eagles.

Prenatal vs. postnatal growth rates

Lack (1968) found a strong correlation between lengths of the nestling and incubation periods for nidicolous land birds. Body size and egg size had only a minor, if any, influence on the relationship. He surmised that perhaps prenatal growth evolved pleiotropically with postnatal growth when the latter was selected for ecological considerations. Case (1978) and Ricklefs (1984b) believe that embryonic and nestling growth may evolve independently.

The effect of body size on incubation periods of eagles is illustrated in Fig. 4A. The relationship is not significant for B2 species ($r = -0.012$, df $= 12$, $P > .05$), but is highly significant for B1 species ($r = 0.705$, df $= 14$, $P < .01$). Egg volume was not correlated with incubation period for either B2's ($r = 0.033$, df $= 12$, $P > .05$) or B1's ($r = 0.354$, df $= 13$, $P > .05$), even though egg volume and body mass were highly cor-

related for both groups (B2: $r = 0.954$, df = 12, $P < .01$; B1: $r = 0.761$, df = 13, $P < .01$). This implies that factors associated with ultimate body size of the species, rather than more proximate factors related to egg size, are responsible for variation in prenatal growth in B1 species. Given the strong dependence of postnatal growth on body mass (Fig. 2), it is not surprising that the length of the incubation period and fledging age are strongly correlated for B1 species ($r = 0.761$, df = 14, $P < .01$), but not at all for B2 species ($r = -0.251$, df = 12, $P > .05$) (Fig. 4B).

Why the relationship between prenatal and postnatal growth should differ between B1 and B2 eagles is enigmatic. Case's (1978) hypothesis relating egg characteristics to feeding ecology of adult seabirds, in particular the frequency with which eggs must be abandoned, cannot be applied to eagles. Although not quantified in detail, there is likely little variation among eagles in their incubation behavior. There is almost always one adult in attendance at the nest and so the eggs are not left uncovered for long periods of time to allow the adults to forage. Although Werschkul and Jackson (1979) did not make any specific predictions about prenatal growth, reduced incubation periods would be selected if sibling competition were an important evolutionary force (see Ricklefs 1984b). Contrary to the sibling competition hypothesis, eagles that are characterized by obligate fratricide are similar to the eagles laying one egg, rather than the B2 species, which lay two or more eggs but for which fratricide is facultative (Fig. 4). Ricklefs (1984b) found that the incubation periods of fratricidal species of boobies (Sulidae) were as long as those of boobies laying only one egg. These results support the idea that factors other than sibling competition have determined patterns of growth.

Growth rate and energy requirements

The energetic consequences of development have been reviewed by Ricklefs (1974, 1983). For several species of birds it appears that the energy cost of growth does not constitute a major component of the total energy requirement of a nestling (Ricklefs 1974, Dunn 1980). Varying the growth rate may not influence the maximum energy requirement, since this peak is often not reached until the young are fully grown (Ricklefs 1974). As modeled by Ricklefs (1969, 1984a) when $GK > M$, (G = the energy requirement for a given amount of growth, K = the growth rate, and M = the energy required for maintenance), the maximum energy requirement occurs before adult size is reached and is directly dependent on K. A reduction in K can therefore reduce the peak energy demand. The Golden Eagle is a species for which $GK > M$, and for which energy for growth is a substantial component of the total energy budget (Collopy 1980). This is also likely to be true for most or all eagles, because M is inversely related to body size. As M decreases with increasing size of bird, the relative importance of growth energy

to the total energy expenditure increases. Eagles that are food limited could thus benefit from reduced energy demands by growing slower. This should be most effective in large species, and may account for the steep slope of the relationship between growth rate and body mass for B1 eagles in Fig. 2, and why the slopes of the regressions for B1 and B2 species are significantly different.

According to the sibling competition hypothesis, variation in growth rate among species should be greater for B1 than B2 species because the former are not subjected to the intense selection pressure of sibling competition (Werschkul and Jackson 1979). Ricklefs (1982) confirmed this prediction. The fledging ages of B1 eagles were also significantly more variable than those of B2 eagles ($F = 3.55$; df = 15, 16; $P < .02$). However, this result is not inconsistent with expectations based on energy considerations. If growth is modified to adjust the energy budget of the brood, e.g., to the foraging ability of the parents, then for a given amount of energy the necessary change in growth per nestling will be relatively greater in small broods than large broods (Ricklefs 1968b).

Energy adjustments through varying growth rates might be expected to be more common in tropical than temperate birds because the former have lower M values (Hails 1983). Tropical passerines grow slower than temperate passerines (Ricklefs 1976), but the extent to which M is reduced in the former is apparently insufficient to account for the degree of reduction in growth rate (Ricklefs 1984a). Although many tropical eagles grow slowly (Fig. 2), there are too few tropical B2's and temperate B1's to test properly the influence of latitude on growth given the overriding effect of brood size.

Form of growth curves

In analyses of intra- and interspecific growth variation, growth rate, whether measured by the growth curve constant K (Ricklefs 1968a) or in more absolute terms (e.g., Drent and Daan 1980), has been the primary concern. Variation in the form of growth curves has received much less attention. Three commonly used growth equations, the logistic, Gompertz, and von Bertalanffy forms, are described in detail in Ricklefs (1967, 1968a). The relative timing of the inflection point is their most important distinguishing feature; specifically inflection of the curve occurs when 30, 37, and 50% of the asymptote level has been reached for von Bertalanffy, Gompertz, and logistic equations, respectively. At equivalent growth rates, logistic growth will be completed the earliest and von Bertalanffy the latest. A general trend in growth observed among birds is for heavy slow-growing species to be characterized by Gompertz and von Bertalanffy curves (Ricklefs 1968a). However, prolonged development and not size appears to be the important determinant of growth form in eagles. Golden, Black, and Crowned eagles are of sim-
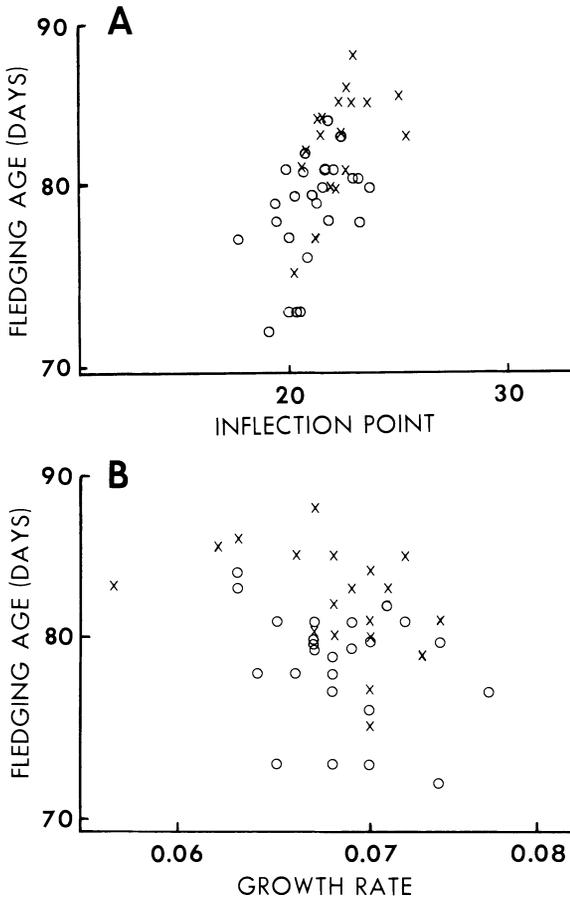
FIG. 5. Relationship between fledging age and (A) inflection point (*t*), and (B) growth rate (*K*), of Gompertz growth equations for male (○) and female (×) Bald Eagles.

ilar size, but each is characterized by a different pattern of growth (Table 1).

The sibling competition hypothesis would predict that selection should favor rapid growth early in the nestling period. Eagles exhibiting obligate fratricide would therefore be expected to show a greater proportion of von Bertalanffy and Gompertz equations than eagles in which fratricide was facultative. This appears to be true for the limited sample in Table 1. However, by the same reasoning, B2 species should have relatively more representatives of the von Bertalanffy and Gompertz growth forms than B1 species laying one egg, which is not the case (Table 1), and in fact likely have far fewer given their faster growth. The Golden Eagle has strong sibling aggression and frequent fratricide (M. Collopy, *personal communication*), yet grows by the logistic growth curve.

Ricklefs (1974) has shown that the energy requirements of a chick can be reduced through changes in the form of the growth curve. The energy demands for maintenance are small when chicks are young but increase with age. The earlier in the nestling period the

maximum energy demand for growth (i.e., the inflection point of the curve) occurs, the lower the peak energy requirement will be. This is unlikely to be of any significance unless $GK > M$, which, as explained earlier, is likely true for eagles. Therefore, it is plausible that in food-limited species there may be selection for curves with early inflection points to minimize energy needs. However, a change to a curve with an earlier inflection point can prolong the development period, and result in a greater total amount of energy that the parents must supply. This may be a sufficient deterrent for some birds, but not eagles. After fledging, eaglets are usually dependent on their parents for food for some time (e.g., 9–11 mo for the Crowned Eagle [Brown 1976]). The length of this period is most likely determined by the time required to develop specialized hunting skills. Therefore, given extended post-fledging parental care, the increased total cost of prolonging the nestling period is likely of little significance. Considering that it is the peak requirement, i.e., the limiting factor of the energy budget, that is reduced through prolonged development, it is plausible that selection would modify the form of growth curves. Thus B1 eagles may have Gompertz or von Bertalanffy growth curves to reduce nestling energy requirements.

I examined the relative usefulness of the form and rate parameters of a single growth equation as indicators of overall development within a species by comparing K and t as predictors of fledging age in Bald Eagles. As shown in Fig. 5A, inflection point was highly correlated with fledging age for males ($r = 0.479$, df = 23, $P < .01$) and females ($r = 0.563$, df = 16, $P < .01$) as well as for both sexes combined ($r = 0.622$, df = 41, $P < .01$). Growth rate was not significantly related to fledging age (Fig. 5B) for males ($r = -0.329$, df = 23, $P > .05$), or for females ($r = -0.336$, df = 16, $P > .05$), and was only marginally so when the sexes were combined ($r = -0.304$, df = 41, $P = .05$). The last comparison is likely significant only because K and t are highly correlated for both sexes separately and when combined (e.g., $r = -0.712$, df = 41, $P < .01$). The timing of growth events therefore appears to be an important consideration when investigating patterns of development, both within and among species (also see Bortolotti 1984b).

Resources available to parents

As mentioned earlier, food habits vary greatly among eagles. This may suggest that the quantity of energy, rather than type of food or hunting method, is a more likely determinant of growth. How often prey are brought to nests is one indicator of the resources available to parents. Data on the number of prey items delivered to nests per day for various species of eagles are summarized in Table 2. The figures in Table 2 are only approximations, as the original data were converted from different methods of observation, and the number of young in the nests and number of hours of

TABLE 2. Number of prey items delivered per day to nests of eagles raising one young (B1) and eagles raising >1 young (B2).

Brood size	Species	No. prey/d	Reference
B1	Harpy Eagle	0.28–0.40	Rettig (1978)
	Crowned Eagle	0.64	Brown (1976)
	Black Eagle	1.2	Gargett (1972)
	Ayre's Hawk-eagle	0.87	Brown (1976)
	Brown Snake Eagle	0.87	Brown (1976)
	Martial Eagle*	0.87	Brown (1976)
B2	Bald Eagle†	5.0–5.8	G. R. Bortolotti (*personal observation*)
	White-tailed Eagle	1.6–3.0	Wille and Kampp (1983)
	African Fish Eagle‡	1.26	Thiollay (1981)
	Golden Eagle	1.3–3.0	Collopy (1984)
	Booted Eagle§	2–7	Steyn and Grobler (1981)
	Long-crested Eagle	2.6	Hall (1979)

* *Polemaetus bellicosus.*

† Based on a mean prey delivery rate of 0.334 prey/h (SD = 0.1916) as observed over 149 observation periods 3–13.5 h in duration.

‡ *Haliaeetus vocifer.* Data on prey capture rate by a breeding pair, proportion brought to nest not specified.

§ *Hieraaetus pennatus.*

daylight were not always specified. However, the data are sufficient to suggest that prey delivery rates for B1 eagles are substantially lower than for B2 eagles. This is true even when considering the average brood size of B2's is greater than (but not twice) the brood size of B1's. The number of chicks to be fed may not be as important a variable in determining the rate of food provisioning as might intuitively be expected. Collopy (1984) found prey delivery rate to be independent of brood size in Golden Eagles. Several raptors characteristically do not adjust the amount of food brought to the nest to the energy demands of the brood, suggesting that prey deliveries are limited by hunting success (Newton 1979). Although a quantitative comparison of energy budgets of B1 and B2 eagles is not possible because relative prey size and other data are not known, the large difference in prey delivery rates between slow-growing B1 eagles and fast-growing B2 eagles strongly suggests that the ability of the parents to provide for their young is an important factor determining growth rate. It seems very likely that fast growth would be disadvantageous for B1 eagles if long periods of fasting occur. A maximum of 13 d between successive food deliveries has been recorded for both Crowned (Brown 1966) and Harpy eagles (Rettig 1978).

Case (1978) observed that slow-growing species are often those whose young are fed large parcels of food at infrequent intervals (also see Ricklefs and White 1981). The prey items of most eagles are usually much larger than the food required for a single meal for the chicks during the growth period. The relative size of meals is not likely to be very different among species, for the chicks are often fed until satiated. The Harpy Eagle usually feeds its young only twice per day from a single carcass that may be fed upon for 3 d (Rettig 1978). By comparison, I observed Bald Eagles feeding their young about once every 2 h in the first 4 wk of the nestling period (and there were as many as 17.4 hours of light per day). Therefore, the number of feed-ings, made possible by the amount of prey captured, is probably a more important factor than the amount eaten per meal. Variation in the degree to which meals can be monopolized by nestlings may explain some of the differences in fratricidal behavior among birds (Mock 1984b). However, the opportunity to monopolize food is likely relatively consistent among eagles given the high prey-size : meal-size ratio.

Factors influencing sibling competition

Studies of a variety of avian species suggest that relatively large body size is a distinct advantage when siblings compete (e.g., Meyburg 1974, Procter 1975, Werschkul 1979, Hahn 1981, Edwards and Collopy 1983). For the Bald Eagles I watched, the size difference between siblings was important in determining the outcome of bouts of sibling aggression. When the size difference was large early in the nestling period (see below), the first-hatched chick (C1) almost invariably pecked, bit, and thrashed the second-hatched chick (C2) into submission. Such aggression was unlike the persistent attacks by C1's characteristic of some obligately fratricidal eagles (Meyburg 1974, Gargett 1978), but instead was more like a contest, often instigated by C2. Aggression early in the nestling period appeared to test or assert dominance, and one chick was always clearly a victor. As the size difference between the siblings decreased, so did the frequency of aggression, and more important, C1 was less frequently dominant and C2 retaliated with aggression rather than adopting submissive postures. In cases where there were two male young or two female young in a nest, a reversal of dominance was observed when C2 surpassed C1 in linear dimensions and mass (Bortolotti 1984c). Therefore, the magnitude of the difference in mass between siblings is likely to be a good indicator of the competitive advantage one chick has over the other and the probability of brood reduction. The death of C2 is unlikely to occur if C1 is not large enough to exclude
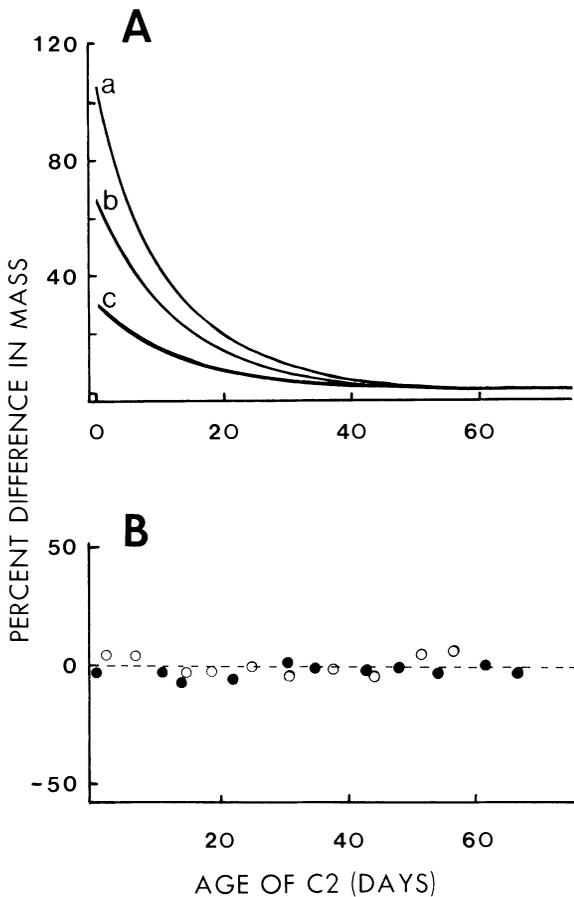
FIG. 6. (A) Percent difference in mass between sibling Bald Eagles, as a function of the age of the younger chick (C2), where the two siblings have identical growth parameters and an interval between hatching of (a) three, (b) two, and (c) one, days. (B) Observed percent difference in mass between siblings in two synchronously hatched broods of Bald Eagles (O a brood with two males, ● a brood with two females). When points fall below the zero-difference line C2 was heavier than C1.

C2 from resources provided by the parents (Edwards and Collopy 1983).

It is presumably through the advantage of larger size that the fast-growing chicks should be selected (via brood reduction) over slower growing nestmates, according to the sibling competition hypothesis. A size difference between nestmates may, however, be the result of many factors. This is particularly true considering that many birds that exhibit sibling competition and fratricide have eggs that hatch asynchronously. The difference in size among nestmates that is attributable to age may be a sufficient determinant of fratricide, so that a further difference attributable to growth rate is inconsequential.

The descriptive model I will now develop examines the influence of hatching asynchrony and growth on the difference in size between siblings, and hence on the likelihood of brood reduction, in two-chick broods.

For simplicity, the chicks are assumed to be of the same sex. The effect of sex-specific growth dynamics on the model is developed in detail elsewhere (Bortolotti 1984c). The curves of relative size difference between chicks, [(mass of C1 − mass of C2)/mass of C2] × 100, were calculated by taking the difference between two Gompertz growth curves defined by the means of the growth parameters a, K, and t of C1 and C2 eaglets, respectively.

Hatching asynchrony. — The simplest scenario for initially illustrating sibling size differences is to assume that the chicks grow equally well, but because of hatching asynchrony they will be different in size when C2 hatches. This is shown in Fig. 6A, using the growth rates of C1 male Bald Eagles for both birds and with three different hatching intervals (intervals >3 d were not observed). Asynchrony creates large sibling size differences by merely offsetting two sigmoid growth curves. The size difference diminishes with age, but the steepness of the decline depends on the degree of asynchrony, as also found for broods of Golden Eagles (Edwards and Collopy 1983). The extremes of size difference between siblings are in the early part of the nestling period, which corresponds to the time when almost all fratricide in eagles occurs (Brown 1976, Edwards and Collopy 1983; G. R. Bortolotti, *personal observation*).

Two clutches of Bald Eagles in my study had both eggs hatch on the same day, albeit a few hours apart. This is the only record I am aware of, for any eagle, of a hatching interval of <1 d. In both cases, one chick was not consistently larger, nor larger to any substantial degree, than its sibling (actual measurements presented in Fig. 6B).

Species-specific growth and hatching asynchrony. — The curves of Fig. 6A are specific to the Bald Eagle. The shape and magnitude of the sibling-size difference curves vary with both the form and rate parameters of the growth equation. The more rapid the growth and earlier the inflection point, the greater the difference between siblings. The size differences are larger and decline more steeply with age for Gompertz and von Bertalanffy growth curves, compared to the logistic curve.

The sibling size differences for the fratricidal eagles, calculated using the species-specific growth curve data (Table 1), are illustrated in Fig. 7A for a hatching interval of 2 d. There is no broad difference between species exhibiting obligate fratricide and those exhibiting facultative fratricide, which supports the idea that a comparison of the two is a valid test of the sibling competition hypothesis. Edwards and Collopy (1983) have shown that eagles that are obligately fratricidal generally have a hatching interval of 3 d, whereas facultatively fratricidal species usually have a 2-d interval. The sibling size difference curve for the modal hatching interval for each species is shown in Fig. 7B. Similar differences between siblings are created by one species with a hatching interval of 2 d, and another species

growing differently with a hatching interval of 3 d. Since the degree of hatching asynchrony is under parental control (the eggs need not be asynchronous at all) the larger hatching interval of species with obligate fratricide may be a response to the slow postnatal growth of their offspring. The bigger the sibling size difference created by the parents, the easier fratricide will be. Fig. 7 shows that growth rate, inflection point, and asymptote of a species' growth curve are as important as the length of the hatching interval in assessing the ramifications of hatching asynchrony. Interspecific comparisons of sibling competition should therefore not be made without knowledge of nestling growth dynamics.

Edwards and Collopy (1983) showed that the difference in size between eggs in a clutch (and hence in hatching mass between nestlings) was larger for eagles where fratricide was obligate than for those where fratricide was facultative. The actual size difference that arises between siblings from relatively small differences in egg size is of little importance to sibling competition compared to the overwhelming effect of hatching asynchrony (Fig. 6A, and see Poole 1982, Ricklefs 1982). The unimportance of egg size relative to asynchrony is further realized when it is known that for some species with brood reduction the last egg laid is the heaviest (e.g., Howe 1976, Rydén 1978, Zach 1982).

Relative growth of siblings. — The previous examples considered siblings with equal growth rates. The following modifications of the model investigate the ramifications of differences in growth between two nestmates, i.e., the sibling competition hypothesis.

Quantitative evidence for late-hatched nestlings growing slower than early-hatched nestlings has been documented for several avian species with hatching asynchrony (Hussell 1972, Siegfried 1972, Howe 1976, Werschkul 1979, Picozzi 1980), but not for eagles. However, it is often suspected that sibling competition inhibits the growth of the youngest chick. Such studies are usually difficult to compare and interpret when we try to determine to what degree growth differentials may be the product of genetics, sibling competition, or other factors such as the distribution of parental care. This is especially true when growth or size of siblings is compared at discrete points in time. Such comparisons ignore the extent to which the results only reflect differences created by hatching asynchrony (i.e., Fig. 6A). Wilcoxon matched-pairs signed-ranks tests revealed that C2 Bald Eagles had lower K ($P < .02$), higher t ($P < .01$), and equal a ($P > .05$) values compared to their nestmates (Bortolotti 1984c). The effect of this slower growth on sibling size differences is illustrated in curve a of Fig. 8. A hatching interval of 2 d is used, for it was by far the most common one I observed (13 of 16 two-egg clutches). The observed lower growth rate and later inflection point of C2 shifts the sibling size difference curve upwards compared to the hypothetical curve of equal sibling growth (Fig. 8, curve b, initially illustrated in Fig. 6A). The pattern in
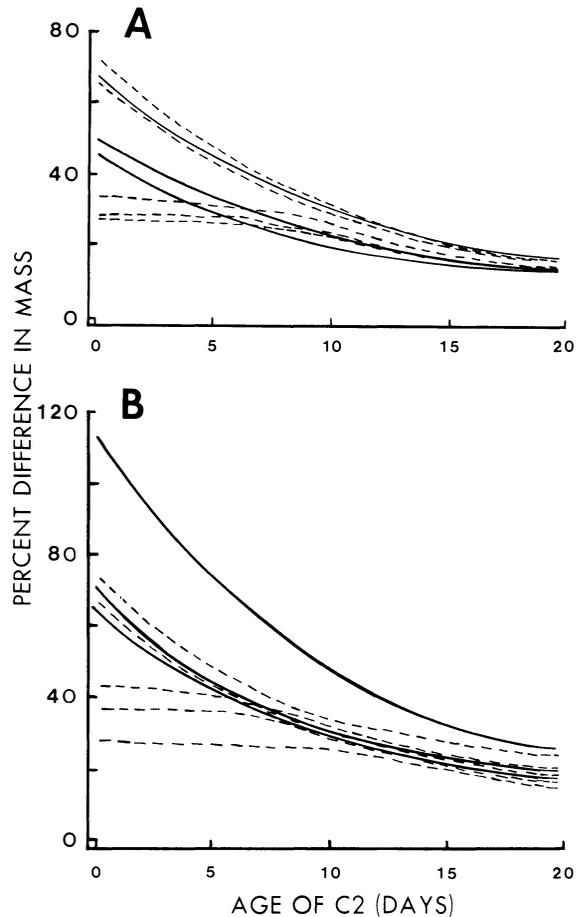

FIG. 7. Percent difference in mass between sibling eagles, as a function of the age of the younger chick (C2), for species characterized by obligate (———) and facultative (– – – –) fratricide (species listed in Table 1), where (A) hatching interval is 2 d for all species, and (B) hatching interval is the modal value observed for each species.

Fig. 8 was consistent among broods regardless of the sex composition. These results, compared to those of the synchronous broods, strongly suggest that hatching asynchrony imposes a disadvantage on late-hatched young, and that the slower growth of C2 is, in this case, probably phenotypic. Similar results were obtained by Werschkul (1979) after manipulating broods of the Little Blue Heron (*Egretta caerulea*). Late-hatched heron chicks grew slower and had higher mortality rates than early-hatched siblings in naturally asynchronous broods, but chicks grew equally well in experimentally synchronized broods. The cross-hatched area between curves a and b of Fig. 8 thus represents the difference in size between siblings that can be attributed to the slower growth of C2; it may provide a means of quantifying the effects of sibling competition. Although phenotypic variation bears no relevance to the sibling competition hypothesis, genetic effects on growth would have the same effect.
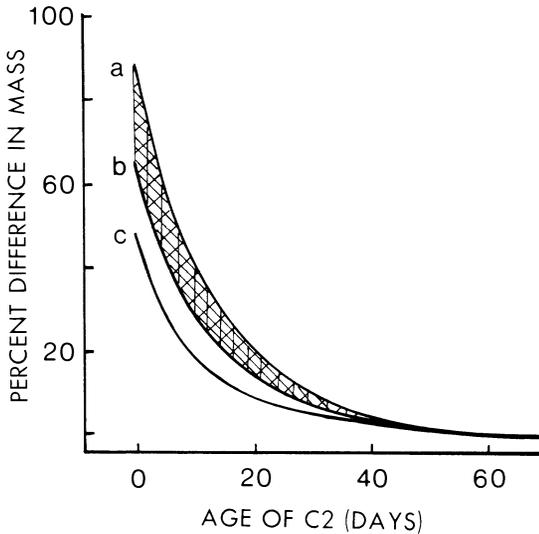
FIG. 8. Percent difference in mass between sibling Bald Eagles, as a function of age of the younger chick (C2), where (a) C1 grows better than C2 (observed pattern), (b) C1 and C2 grow equally well (possible hypothetically), (c) C2 grows better than C1 (unlikely hypothetically), for a hatching interval between eggs of 2 d. The cross-hatched area represents the difference in size between siblings that can be attributed to the slower growth of C2 compared to C1 in the observed situation.

Ricklefs (1982) underestimated the changes differential growth could have on the relative size of siblings, for he assumed a linear relationship between changes in K and changes in sibling size differences. C1 Bald Eagles had only 3.5% larger K values than C2's, yet when C2's were 0, 7, and 15 d old, for example, C1's were an extra 23, 15, and 9% larger, respectively, above and beyond the difference attributable to age. However, as recognized by Ricklefs (1982), the potential differences in size related to differences in growth are still much less than those imposed by hatching asynchrony. Curve c of Fig. 8 represents the size difference between siblings if the relative growths of C1 and C2 were exactly reversed. This hypothetical faster growth of C2 would not overcome the competitive disadvantage of late hatching. Given the apparent relative weakness of variation in growth rate in influencing the probability of fratricide, the strength of sibling competition in selecting for rapid growth is questionable.

The sibling competition hypothesis may not be any more plausible for species having synchronous hatching than it is for species with asynchronous hatching. The difference in size among siblings that would arise from growth differentials may not alter the probability of fratricide. Even if large sibling size differences could be created, it is not known how often parents could provide enough energy for the full genetic growth potential of their offspring to be expressed. It does not seem reasonable to assume that a chick would be able to grow faster than its siblings under all levels of food

provisioning (Richter 1983). Faster growth requires additional food. If food is limited then growth of all nestlings in the brood may be restricted to a rate below their maximum potential. If adequate resources were available to support fast growth, they would likely also be sufficient to raise the entire brood to fledging and hence natural selection would not operate.

CONCLUSIONS

A dichotomy is apparent in the variation in growth among eagles. Although not distinctly different in body size, morphology, mode of development, phylogeny, or food habits, species that raise only one young show patterns of pre- and postnatal growth unlike those of species raising larger broods. The latter species grow at a rate expected of birds of their body size. The apparent reduction in growth rate and the typical growth form of B1 species suggest growth may be evolutionarily flexible in light of environmental constraints. As summarized in Fig. 1, the data on eagles suggest that factors other than sibling competition are the important determinants of growth. The sibling competition hypothesis was proposed on the basis of the correlation between brood size and growth rate, but without evidence supporting the plausibility of the proposed mechanism of selection. Not only is the strength of sibling competition as a selective force questionable, but the underlying assumptions regarding the relative growth of siblings at different levels of food provisioning may not be realistic. Although the overriding suggestion in this paper has been that poor resource availability may have been responsible for reduced growth rates of B1's, parental reproductive effort, perhaps as dictated by food supply, may be the primary target of selection (Ricklefs 1983). Given the paucity of information for most eagles on basic breeding biology and population demography, such an hypothesis may remain untestable for some time. The patterns of growth delineated in this paper are, however, consistent with predictions of the food limitation hypothesis. That these patterns are evident in eagles may largely be a product of the size of the birds, rather than any unique ecological or phylogenetic trait. Adjusting the rate and form of growth, as a means of reducing energy requirements, is only feasible if the energy devoted to growth assumes a substantial proportion of the total energy budget. This may be particularly true for large birds, given the negative correlation of metabolic rate and body size. The fact that not all eagles have reduced growth rates suggests that certain costs, perhaps mortality independent of brood size, exceed the benefits of lower energy requirements for those species.

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