

OBLIGATE AND FACULTATIVE BROOD REDUCTION IN EAGLES: AN EXAMINATION OF FACTORS THAT INFLUENCE FRATRICIDE

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ABSTRACT.—Fratricide in eagles (Accipitridae: Accipitrinae) is either obligate [second hatched nestling (C2) always dies] or facultative (C2 occasionally dies) and appears to be a function of relative size differences between siblings. Several factors, including time between hatching, differences in hatching weights, and possibly the sex of the nestling in conjunction with its hatching sequence, influence size difference. Size differences are modified further by feeding rates of young by adults. These factors determine the relative differences in locomotor development and coordination and thus the ability of the first-hatched nestling to control access to and monopolize parent-provided resources. Significantly greater ($P < 0.0001$) within-clutch volume differences (an indicator of disparity in hatching weight) and greater time between hatching (mode of 3 versus 2 days) are found in eagles in which fratricide is obligate (three species) than in those in which fratricide is facultative (eight species). We suggest that these differences are proximate mechanisms that account for observed differences in the frequency of fratricide in eagles. Although size difference is determined in part by the sex and hatching sequence of the nestling, the role of offspring sex in fratricide is not clear. Received 1 November 1982, accepted 21 March 1983.

In many species of birds the older, dominant nestling (hereafter referred to as C1) is instrumental in causing the death of its younger, subordinate (C2) sibling [e.g. South Polar Skua (*Catharacta maccormicki*), Proctor 1975; Brown Booby (*Sula leucogaster*), Dorward 1962; many species of raptors, Meyburg 1974, Stinson 1979]. The death of C2 may result from direct aggression by C1, but more often indirect harassment and intimidation prevent C2 from obtaining the resources necessary for growth and survival (e.g. food, brood time). This form of brood reduction, termed fratricide, is observed in many birds of prey. Within this group, it is most common in eagles (Accipitridae: Accipitrinae) with a clutch size of two. Published literature suggests there are two categories of fratricide: an obligate form where C2 invariably dies as a result of fratricide, and a facultative form where C2 occasionally dies (Table 1).

The relative size difference of siblings (calculated as $Dt/weight$ C2, where Dt = sibling weight difference) is an important proximate

factor leading to fratricide. Size difference determines the ability of a nestling to dominate and outcompete its smaller sibling(s) (Lack 1954). As nestlings age and gain weight, size difference typically decreases. We suggest that fratricide becomes probable when size difference increases and exceeds a hypothetical fratricide threshold. Before this threshold is reached, size difference is such that dominance is indeterminate. This does not imply a lack of dominance when only slight differences exist (see Poole 1979) but rather that the outcome of sibling aggressive interactions may vary. Neither sibling can effectively dominate the other. Fratricide is unlikely unless size difference is great enough to ensure exclusion of C2 from parent-provided resources. For theoretical considerations of fratricide see O'Connor (1978) and Stinson (1979).

Size difference is a function of several factors acting in concert. Here, using Golden Eagles (*Aquila chrysaetos*) as a test species, we examine several factors that we feel are important in understanding fratricide in eagles. We have used data from the literature, museum specimens, field studies, and, where available, from other eagles. Comparisons also are made between the eagles grouped in the two categories

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TABLE 1. Species of eagles exhibiting either obligate or facultative fratricide as defined in text.

Species	Type of fratricide ^a	Hatch interval ^b	Source
Crowned Eagle (<i>Stephanoaetus coronatus</i>)	O	3	Brown and Amadon (1968)
Verreaux's Eagle (<i>Aquila verreauxii</i>)	O	3	Meyburg (1974) Brown and Amadon (1968)
Lesser-spotted Eagle (<i>A. pomarina</i>)	O	3-4	Meyburg (1974) Brown and Amadon (1968)
Greater-spotted Eagle (<i>A. clanga</i>)	F	2	Brown and Amadon (1968)
Tawny Eagle (<i>A. rapax</i>)	F	"several days"	Brown and Amadon (1968)
Imperial Eagle (<i>A. heliaca</i>)	F	2	Brown and Amadon (1968)
Golden Eagle (<i>A. chrysaetos</i>)	F	2	Brown and Amadon (1968) This study
Wedge-tailed Eagle (<i>A. audax</i>)	F	1-4	Brown and Amadon (1968)
African Hawk Eagle (<i>Hieraetus fasciatus</i>)	F	3	Brown (1952)
Booted Eagle (<i>H. pennatus</i>)	F	"several days"	Brown and Amadon (1968)
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	F	2	Brown and Amadon (1968)

^aO = obligate, F = facultative.

^bRepresents mode in days.

of fratricide to determine whether or not possible differences in proximate mechanisms can account for the observed differences in the frequency of fratricide.

METHODS AND RESULTS

Hatch interval.—Comparing the categories of fratricide reveals that, in general, hatching interval is greater when fratricide is obligate rather than facultative (Table 1). The effect of time between hatching on size difference can be seen in a comparison of 1-, 2-, and 3-day hatch intervals in 12 broods of Golden Eagles studied in southwestern Idaho (Fig. 1). Nestling weight measurements, used to determine size difference, were taken every 4-6 days during brood rearing (Kochert 1972, Collopy 1980). The percentage size difference was calculated from sibling weight difference/weight C2. Note that the peak value in size difference increases as time between hatching increases. Although not examined here, the intensity of sibling aggression is probably greater when size difference is small and dominance less determinate (D. Mock, pers. comm.). A large difference

establishes dominance with a minimum of aggressive interactions. Both Meyburg (1974) and Newton (1977) consider hatch interval and its effect on size difference an important factor in fratricide.

One result of hatching asynchrony in eagles is the establishment of a feeding hierarchy among the young whereby C1 can control access to the female and feed first (Meyburg 1974, Collopy 1980). The presentation of food to the young in small, easily controlled bits allows C1 to deny C2 access to the female and to ensure adequate food for itself. As C1 becomes satiated, its response to a begging attempt by C2 becomes less aggressive. An analysis of time-lapse photography and over 1,950 h of brood-rearing observations from blinds showed that parents made no effort to distribute food equally between the nestlings and did not interfere where C1 responded aggressively toward C2 (Collopy 1980). Thus, if feeding rates are low, siblings do not receive equal shares of food, and C2, receiving less, will exhibit slower growth than C1. Relative size difference can rapidly increase.

Hatching weight.—Data on differences in

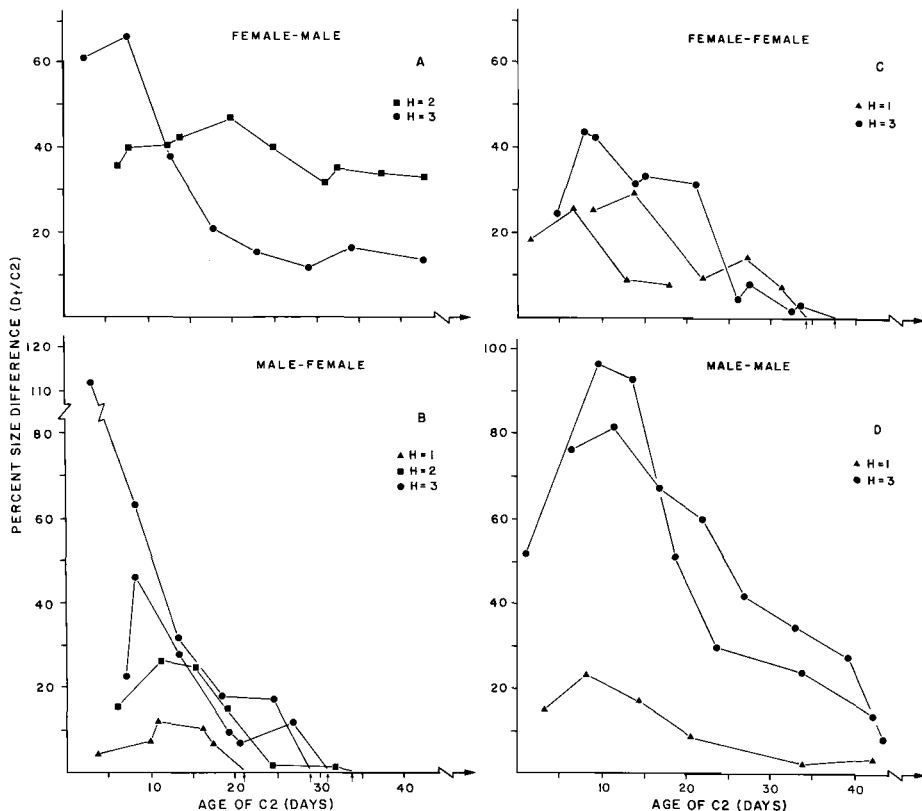


Fig. 1. Effect of nestling sex, hatching sequence, and time between hatching on sibling size difference in 12 broods of Golden Eagles in southwestern Idaho. Arrows on horizontal axes indicate point in a particular brood where siblings approach equality in size. Note vertical scale difference in Fig. 1b.

hatching weights of sibling eagles are limited. The lower relative hatching weight of C2 is documented for Verreaux's Eagle (*Aquila verreauxii*; Gargett, unpubl. data) and the African Hawk Eagle (*Hieraetus fasciatus*; Meyburg 1974) and is suggested for other large eagles (Newton 1977). One possible indicator of hatching weight is egg volume (see Parsons 1970, Howe 1976). Egg-volume data were obtained from museum specimens for eight species of eagles exhibiting facultative fratricide and three species in which fratricide is obligate. Volume was estimated from the equation $V = 0.51LB^2$, where L = length and B = breadth of the egg (Hoyt 1979). The equation (volume difference between eggs/volume smaller egg) was used to calculate the percentage of volume difference within each museum clutch examined (Table 2).

To test the effect of difference in hatching

weight properly, one should know the laying sequence in each museum egg set. Except for Verreaux's Eagle, however, this information is unavailable. Thus, our results represent a magnitude of volume difference within a clutch, and, although inappropriate for testing hypotheses regarding hatch-weight differences in particular species, the results can be used to compare potential hatch-weight differences between eagles in which fratricide is obligate and those in which it is facultative. This comparison shows that significant differences do exist: those species in which fratricide is obligate exhibit greater within-clutch volume difference than do those defined as facultative ($n = 11$, $P < 0.0001$, Kruskal-Wallis single-factor test).

Nestling sex and hatching sequence.—In a brood in which both nestlings obtain sufficient food to maintain maximum growth, size difference peaks slightly after C2 hatches, then decreases

TABLE 2. Analysis of within-clutch egg-volume difference for eagles exhibiting fratricide.

Type of fratricide ^a	Species	n ^b	Mean percentage of volume difference	SE
O	<i>Aquila pomarina</i>	34	13.04	0.27
O	<i>A. verreauxii</i>	49 ^c	12.08	1.00
O	<i>Stephanoaetus coronatus</i>	10	11.93	0.26
F	<i>A. chrysaetos</i>	36	5.37	0.66
F	<i>A. heliaca</i>	36	4.91	0.55
F	<i>A. audax</i>	20	4.84	0.74
F	<i>Hieraaetus fasciatus</i>	30	4.83	0.60
F	<i>A. rapax</i>	35	4.36	0.67
F	<i>Haliaeetus leucocephalus</i>	35	3.57	0.46
F	<i>A. clanga</i>	15	3.52	0.78
F	<i>Hieraaetus pennatus</i>	14	3.09	0.50

^a O = obligate, F = facultative.

^b Number of two egg clutches examined.

^c 42 clutches from Gargett (unpubl. data).

as the nestlings age and gain weight. The rate at which size difference decreases, however, depends in part on the sexual composition of the brood and the sequence in which the nestlings hatch (Fig. 1). To determine nestling sex, we used a combination of body weight and foot-pad length (Kochert 1972, Collopy 1980). A female-male sequence is relatively shallow in slope, and, due to size dimorphism, the difference does not approach zero (Fig. 1a). In contrast, a male-female sequence results in a size difference of short duration and a relatively steep slope (Fig. 1b). By 35 days of age females typically had overtaken and passed male siblings in weight. Single sex broods (Figs. 1c, d) were intermediate in value. Similar results are predicted for other dimorphic eagles.

The duration of the peak value in size difference affects the probability of fratricide occurring. In Golden Eagles, peak size differences occurred 6-15 days after C2 hatched, a time frame coinciding with our three observations of fratricide in this species. Before the occurrence of fratricide, size differences at the last nest visit before death equaled 98% [hatch interval (H) = 5 days], 251% (H = 3), and 329% (H = 3). The small size difference in case one may be a result of limited sampling. C2 was 3 days of age when weights were taken, and, when the nest was visited 6 days later, C2 was dead. Remains on the nest and previous observations of active aggression by C1 toward C2 suggested fratricide. In case two, fratricide occurred when C2 was 9-13 days of age. The size

difference in case three is based upon a weight measurement taken 1 day after C2 died (age at death = 14 days, calculated from analysis of time-lapse photography). Examination of both the dead nestlings revealed numerous scars on and around the head, neck, and back, indicating fratricide had occurred. Necropsies performed on C2 in cases two and three revealed that the nestlings were males. Based upon body weight and foot-pad length measurements, the two nestlings that subsequently fledged were female. The third was a male that hatched 5 days before his sibling.

DISCUSSION

The differential mortality associated with asynchronous hatching is considered an adaptive mechanism that increases parental reproductive success when food is limited (Lack 1954, 1968, but see Clark and Wilson 1981). Benefits associated with fratricide as a means of brood reduction will vary from year to year. For this reason mechanisms capable of yearly adjustment are adaptive. Year-to-year adjustment of hatch interval, differences in sibling hatch weights, and possibly manipulation of offspring sex and hatching sequence can establish conditions each breeding season whereby fratricide can be facilitated and parental reproductive success maximized.

Manipulation of offspring sex and hatching sequence (see Howe 1976, Ankney 1982) may be one adaptive mechanism that can maximize

yearly reproductive success. A comparison of Figs. 1a and b shows that a female-male sequence increases not only size difference but also its duration. This suggests that fratricide may be more likely in a female-male brood. Breeding females, if able to "perceive" current environmental conditions, may manipulate offspring sex and hatching sequence in a manner that facilitates fratricide if brood reduction becomes necessary. In years of poor prey availability, a second-hatched male, whose growth rate decreases as a result of decreased feeding opportunities, rapidly increases sibling-size difference. Requirements for fratricide can be quickly met, and brood reduction can occur before parents invest too much energy into the younger sibling.

In addition to the possible manipulation of offspring sex to facilitate fratricide, females that overwinter poorly and who are taxed energetically may increase the time between hatching. The poorer a female's condition, the longer it takes to produce an egg (King 1973). The increase in hatch interval increases sibling-size difference, establishing a situation whereby fratricide is easily facilitated if prey availability for the nestlings is poor.

Greater within-clutch differences in egg volume (indicating greater disparity in hatching weight) and longer hatch intervals are major differences between species in which facultative and obligate fratricide occur. The extra day of growth, coupled with a greater difference in sibling hatch weight, predispose the brood to fratricide. Why these differences evolved is unknown and will remain speculative. The result is a set of proximate mechanisms that establish conditions whereby the fratricide threshold is invariably exceeded.

The death of C2 before it has any possibility of fledging poses interesting evolutionary questions as to the significance and continued maintenance of the second egg. The prevalent hypothesis is that C2 acts as insurance in case C1 fails to hatch or suffers early mortality (Meyburg 1974, Stinson 1979). An additional factor helping to maintain a two-egg clutch may be the relatively low cost of producing the second egg. Of six major groups of birds examined by Ricklefs (1974), the energetic cost of egg production is lowest in raptors. Smaller second eggs may be a result of a conflict between the requirements for an egg large enough to produce viable offspring yet small enough to en-

sure that fratricide will occur and minimize energy waste. The greater reproductive success associated with a two-egg clutch may counterbalance any selective pressure toward reducing clutch size from two to one. These factors suggest that, if parents cannot raise more than one offspring, it may be more adaptive to evolve mechanisms that virtually ensure that the brood will be reduced through fratricide rather than through reduction in clutch size.

On the basis of Hamilton's (1964) fitness argument, sibling aggression and parental behavior suppressing these interactions should be apparent. This suggests, due to the active participation of C1 in the death of C2 during fratricide, the possibility that a parent-offspring conflict (*sensu* Trivers 1974) might exist. Parental suppression of sibling aggression is reported for South Polar Skuas, Sandhill Cranes (*Grus canadensis*), and both White (*Sula dactylatra*) and Brown (*S. leucogaster*) boobies (cf. O'Connor 1978). This led O'Connor (1978) to conclude that discrimination against smaller nestlings is practiced only by larger siblings and not by adults. It is important to note, however, that the parents' ability to suppress siblings aggression in these species depends upon adequate space for segregation of the young. Furthermore, suppression of sibling agonistic behavior through brooding (Young 1963, Meyburg 1974) is temporary and does not necessarily prevent the occurrence of fratricide or imply that brooding is part of a parental strategy to decrease sibling aggression.

In contrast, that adult Golden Eagles ignore aggressive interactions between siblings and make no attempt to distribute food equally suggests, at least for this species, that no parent-offspring conflict exists. Similarly, Steyn (1973) reports that adult Tawny Eagles (*A. rapax*) make no attempt to distribute food equally among the young, nor do adult Great Egrets (*Casmerodius albus*) or Great Blue Herons (*Ardea herodias*) actively suppress the aggressive interactions of siblings (D. Mock pers. comm.). In addition, adequate space for segregation is lacking in cliff- and tree-nesting species. It is more likely that the aggressive interactions leading up to fratricide serve the best interests of the parents.

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