THE IMPORTANCE OF JUVENILE CANNIBALISM IN THE BREEDING BIOLOGY OF CERTAIN BIRDS OF PREY

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For the majority of birds it is manifestly of considerable importance to synchronize, so far as is possible, the hatching date of their eggs. Indeed, this is essential if the entire brood is to leave the nest at approximately the same time, which, in most species, is necessary if they are all to survive. The approximate synchronization of the hatching date is, of course, normally effected by postponing full-time incubation until the clutch has been nearly, or wholly, completed; but it may be further assisted if the more recently laid eggs require a slightly shorter time to hatch than those deposited earlier (See Jourdain, *in* Witherby *et al.*, **1**: xxi; 1938).

As a uniform hatching date is indubitably a desirable feature in the breeding biology of most birds, why is it that with the majority of raptors there is no synchronization in the hatching of the clutch? On the contrary with many of them, intervals of one, two, or more days commonly occur between the birth of each nestling. In large-brooded species, since incubation usually starts with the first egg laid, this may even result in differences of a fortnight or more between the ages of the first and last hatched nestling.

What are the advantages gained by graduating the ages of their young in this way? I suggest, at any rate so far as the larger-brooded raptors are concerned, that the habit is beneficial for the following reasons. First, by "staggering" their ages, the task of sustaining a large and growing family of carnivorous young, instead of becoming progressively more difficult and perhaps ultimately impossible, is simplified, and to a great extent eased, by being spread over a prolonged period. And, secondly, as it is eugenically preferable to rear, let us say, one or two healthy well-nourished progeny rather than six or seven weaklings, this "staggering" is of the highest importance since it offers perhaps the only satisfactory way—namely by controlled cannibalism —of numerically reducing the family to a feedable size when this has become vitally necessary owing to a food shortage. As the food supply of some of the owls—and this is especially true of *Asio flammeus*—is often largely dependent on fluctuations in the population of certain rodents, a ready and rapid means of adjusting the size of the brood to the amount of food available is clearly desirable.

Without a marked disparity in the age and size of the fledglings, fratricide would be virtually impossible and consequently no such

rapid adjustment could take place—hence the need for "staggering" their ages.

This very interesting phase in the life history of many raptors has been largely neglected by ornithologists and in consequence literature on the subject is somewhat meagre. Except for a short paper by Wendland (1958), the survival value derived from the elimination of redundant fledglings appears to have been ignored, even when juvenile cannibalism has been mentioned.

This dearth of authentic records is perhaps understandable, for should a nestling disappear unaccountably from a nest that is being watched, the observer will almost certainly presume that, after death from lack of food or some natural cause, its body has been removed by one of its parents. That was apparently the conclusion arrived at by A. A. Saunders (quoted by Bent, 1937: 82) when he found that the two youngest members of a brood of Marsh Hawks (*Circus cyaneus hudsonius*) had inexplicably vanished from a nest. Two days before this discovery he had remarked that the oldest birds were about three times the size of the latest hatched nestlings, which were, of course, the ones that had disappeared. Failing detection *in flagrante delicto,* which is extremely unlikely, it is only when the remains of a body—usually the beak and part of the skull—has been actually found in a nest or in one of the nestling's castings, that cannibalism can be definitely established, and such discoveries are necessarily very few.

Thus, although circumstantial evidence indicates that fratricide (which apparently is almost invariably followed by cannibalism) occurs, either commonly or occasionally, in most birds of prey, I have come across what seem to me convincing records only in the following species:

Common Buzzard (*Buteo buteo*); Rough-legged Buzzard (*Buteo lagopus*); Swainson's Hawk (*Buteo swainsoni*); Red-tailed Hawk (*Buteo jamaicensis borealis*); Red-shouldered Hawk (*Buteo lineatus*); Golden Eagle (*Aquila chrysaetus*); Bald Eagle (*Haliaeetus leucocephalus*); Kestrel (*Falco tinnunculus*); Lesser Spotted Eagle (*Aquila pomarina*); Verreaux's Eagle (*Aquila verreauxi*); African Hawk Eagle (*Hieraetus ayresi*); Crowned Hawk Eagle (*Stephanoaetus coronatus*); Goshawk (*Accipiter gentilis*); Peregrine (*Falco peregrinus*); Hen Harrier (*Circus c. cyaneus*), and its American counterpart, the Marsh Hawk (*Circus cyaneus hudsonius*); Marsh Harrier (*Circus aeruginosus*); and, among the nocturnal birds of prey, in the Short-eared Owl (*Asio flammeus*); Long-eared Owl (*Asio otus*); Great Horned Owl (*Bubo virginianus*); Barn Owl (*Tyto alba*); and Philippine Grass Owl (*Tyto capensis amauronota*).

Krambrich (1954) has published a short note on a single instance of cannibalism in the Honey Buzzard (*Pernis apivorus*), but as that species is largely insectivorous this would appear to be a very unusual event, and for that reason I have purposely omitted it from my list of "convincing records."

Buzzards. In the Common Buzzard (*Buteo buteo*) juvenile cannibalism is of frequent occurrence, as the observations of J. H. Salter (1904) and H. A. Gilbert and A. Brook (1924) and others clearly indicate. Referring to this hawk, Salter writes—"The young are . . . hatched at intervals of one or perhaps two days. The nestling which is first hatched is naturally the strongest, and the result is frequently a family tragedy. It appears to be quite the usual thing for the first-born to kill one, if not both of his younger brothers. . . . While three eggs are frequently laid, the bird (in some districts) never brings off three young. This appears to be the case in the hills, but in the lower and more fertile valleys where food is abundant, I have known several instances in which three young were reared." That cannibalism had followed fratricide in at least one instance was definitely proved by A. Brook (1924) when he found the claw of a nestling among other remains in a Common Buzzard's nest.

Very similar observations have been made in Germany by Schmaus (1938) and Wendland (1958). The former (as quoted by Lack, 1947), states that out of fourteen nests of this species found during the years 1932-36, in only four instances were all of the young hatched successfully reared. It is of interest to note that these successes all occurred during a year when mice were unusually abundant. Wendland (1958) declares that when the population of field mice is inadequate sometimes as many as a third of the Common Buzzards hatched fail to reach maturity.

Apparently cannibalism also figures prominently in the domestic economy of the Rough-legged Buzzard (*Buteo lagopus*). E. K. Barth (1952) in the English summary of his paper on the breeding biology of that bird in Finland says "I have observed that the older and stronger young of the Rough-legged Buzzard ate the later hatched weaklings"—a statement which would seem to imply that juvenile cannibalism is normal, rather than exceptional, in that species.

Again we learn from Criddle (*in* Bent, 1937: 154) that in only one out of six nests of the Eastern Red-tailed Hawk (*Buteo jamaicensis borealis*) did the parents succeed in rearing more than one young "though more were hatched in every instance."

Although the Craigheads (1956) make no mention of cannibalism

in their book, from the statistics they give of juvenile mortality in the nests of the Red-shouldered and Swainson's Hawks (*Buteo lineatus* and *B. swainsoni*), it is evident that the practice must be of common occurrence in those two species: in both the mortality after hatching is stated to be roughly 40%.

Harriers. We have definite proof that cannibalism is occasionally, if not frequently, practiced among the fledglings of the Hen Harrier (*Circus c. cyaneus*), which, significantly, is one of the larger brooded raptors. David Bannerman (1956) cites the Norwegian naturalist, Dr. Y. Hagen, as having found on three separate occasions the remains of victims in as many different nests of this Harrier, and that over a period of nine years out of 102 young of this species hatched only seventy succeeded in reaching maturity. In view of Hagen's discoveries is it not permissible to ascribe at least a proportion of this heavy mortality to cannibalism? Conclusive proof that it has occurred, at least once, in a brood of Marsh Harriers (*Circus aeruginosus*) comes from J. Vincent (1936).

Eagles. It is difficult to understand in what way eagles, which lay only two, or at most three, eggs, can possibly benefit by the fratricidal tendencies so commonly found in their young. With most species it is apparently usual for the younger eaglet to be killed by the first born. The relentless pugnacity with which an older nestling Golden Eagle (*A. chrysaetus*) will persistently attack its younger and weaker nestmate has been described by Seton Gordon (1956) and others, while very similar behavior has been recorded by E. G. Rowe (1947) for the young of Verreaux's Eagle (*A. verreauxi*) in Africa. A. C. Bent (1937: 340–341) writing of the Bald Eagle (*Haliaeetus leucocephalus*), whose young seemingly hatch at intervals of a few days, remarks that "Although often two, and sometimes three eaglets are hatched, the larger number is seldom raised to maturity and often only one eaglet lives to grow up." Of the White-tailed or Gray Sea-Eagle (*H. albicilla*) Jourdain (*in* Bent, 1937: 315) says the smaller young is bullied and not infrequently dies. V. Wendland (1958) says that it is well known that the first hatched nestling of the Lesser Spotted Eagle (*A. pomarina*) will almost invariably cause the death of the later hatched nestmate. Between 1928-38 Wendland examined twenty-eight eyries of this eagle and of these, eleven were kept under close scrutiny. He tells us that the hatching intervals between the two eggs laid were from three to four days. The younger nestling always disappeared when from three to four days old.

Among the eagles studied by Leslie Brown (1955) in Africa, he found

that only the African Hawk Eagle (*Hieraetus ayresi*), one species of Crowned Eagle (*Stephanoaetus coronatus*), and Verreaux's Eagle (*Aquila verreauxi*) regularly laid two eggs. Out of seven cases where two eaglets hatched, both survived in only two nests. It is said that the fighting instinct in young eaglets ceases after the first few weeks and that thereafter two or more fledglings will live amicably together. I believe this to be also true of other birds of prey whose nestlings are prone to fratricide.

Owls. With some of the owls juvenile cannibalism is apparently a prevalent habit. Its incidence has been proved in the Barn Owl (*Tyto alba pratincola*) by the discovery of osseous remains in the castings ejected by some of the surviving nestlings (Hawbecker, 1945); while similar proof is forthcoming for the Great Horned Owl (*Bubo virginianus*) (Errington, *et al.*, 1940: 836, 844, *cf.* 794). Amadon and Jewett (1946) writing of a Philippine Grass Owl (*Tyto capensis amauronota*) nest, explain the loss of one of the two fledglings it contained as "probably eaten by the other young or the female."

My own observations suggest that juvenile cannibalism is of frequent occurrence in the Short-eared Owl (*Asio flammeus*). In regard to that species, I am satisfied that in certain circumstances, namely when there is a dearth of prey, the removal of the weaker members of the brood is not only desirable but has a definite survival value. On the other hand, in times of plenty it would, if practiced, be just the reverse, since it would then unnecessarily curtail a natural increase in the birds' population. I believe that to prevent that from happening when conditions are propitious, Nature has evolved a simple method by which the fratricidal tendencies of the older nestlings are to some extent controlled. This is achieved by the parents providing, when rodents are sufficiently abundant, a constant and easily accessible supply of surplus food for the young when hungry. This surplus, or "control" food (as I shall henceforward call it) is, of course, supplementary to that brought directly to the brood. Instead of being given at once to the fledglings this is placed at some little distance from them—usually about three or four inches from the edge of the nest. The function of this would appear to be twofold: first, the intervening space is seemingly sufficient to deter the nestlings from eating it until impelled to do so by hunger; secondly, it restricts its consumption to the older, that is to say, to the potentially fratricidal, members of the brood, since they alone will be sufficiently developed to be physically capable of reaching it.

It was while studying the breeding habits of two pairs of Short-eared

(*Above*) Nest of Short-eared Owl (*Asio flammeus*), showing two larders for storing "control" food. Note the body of a field vole in one of the larders. The three youngest members of the brood have already disappeared, probably killed and eaten by their larger brethren. (Photo. by C. Ingram.)

(*Below*) Barred Owl (*Strix varia*) incubating on ground nest. Seven-Mile Fire Tower, Everglades National Park, January, 1957. (Photo by Fred K. Truslow.)

Owls on one of the more northern of the Orkney islands that I came to the conclusion that the distance from the edge of the nest at which the "control" food is placed is of functional importance and not merely a matter of chance. It so happened that both of these owls' nests were so closely encircled by a dense growth of coarse grass that there was virtually no space round their perimeters upon which the old birds could lay the "control" food. Consequently, to enable it to be placed at what I presume is the correct distance from the nest, the adults had in both cases been obliged to excavate a small cave, or "larder," in the surrounding wall of vegetation. These "larders" were in the form of a neatly made recess some five or six inches in depth. It was in these that the "control" food, here composed entirely of small rodents, was always placed. Incidentally, the bodies of these rodents, when more than one, were invariably laid side by side and were therefore always at approximately the same distance from the edge of the nest.

One of these Orcadian nests had been provided with two such "larders" (Plate 7 *above*), the other with only one. I understand where the surrounding vegetation is of a different nature and sufficiently open to allow the control food to be laid at the requisite distance on the bare ground fully exposed to view, these larders are dispensed with.

From the first of these two nests, according to the warden of the bird sanctuary who showed it to me, three owlets had previously disappeared, leaving only four survivors; from the second nest, two out of a brood of eight vanished during the first few days of my visit. Thereafter, throughout my stay on the island, no further losses were noted (Ingram, 1954).

The apparently mysterious disappearance of these five owlets can, I feel confident, be attributed only to cannibalism, since it is inconceivable that the old birds, ceaselessly on the alert, would have permitted their removal by any of the local predators, which were here chiefly composed of Lesser Black-backed and Herring Gulls (*Larus fuscus* and *L. argentatus*). In any case, had any of those birds succeeded in raiding the nests, it is very unlikely that they would have deliberately selected for their prey the smallest and least conspicuous of the nestlings, which in both cases were the ones that had disappeared.

I suggest that the subsequent cessation of these cannibalistic activities was mainly due to two causes: (a) the approximation in size of the surviving fledglings as they grew older and after the elimination

of the youngest or smallest members of the brood, and (b) the apparent rapid increase in the numbers of field voles (*Microtus agrestis*) as the summer advanced—an increase which enabled the adults to maintain a more or less uninterrupted supply of "control" food.

Kenneth Richmond (1958), writing of this species, describes a truly remarkable incident. Wishing to photograph a Short-eared Owl in natural surroundings, he erected a hide near one of their nests containing a brood of nine young. As the adults were reluctant to return to the nest while the hide was there, after waiting patiently for an hour and a half, Richmond decided to abandon his project and remove the offending hide. Before departing he counted the nestlings: there were now only six! "The discovery," he says, "left me gaping. But this was impossible! After all, I had been watching them at a distance of only a few feet, never once taking my eyes off them for the best part of two hours. Still there it was: instead of nine, there were now only six." Although Richmond does not attribute the mysterious disappearance of these three fledglings to cannibalism, I cannot conceive how there can possibly be any other explanation. The fact that the old birds were denied access to the nest for two hours or more apparently upset the normal rhythm of their domestic behavior. During that period, admittedly not a very long one, they were unable either to brood their young or to bring them any food—both factors which would have discouraged the cannibalistic tendencies of the larger fledglings.

In some respects, the breeding habits of the Snowy Owl (*Nyctea scandiaca*) appear to be not unlike those of the Short-eared Owl. It also builds its nest on the ground and in a similar manner lays its eggs—sometimes numbering as many as nine or ten—at irregular intervals over a long period, so that its young may vary in age and size from a half-grown fledgling, perhaps fourteen to fifteen days old, to an unhatched embryo. O. I. Murie (quoted *in* Bent, 1938), expressed surprise at the high mortality he found among the young of this species. He notes that "most of the broods numbering seven or eight were eventually reduced to four or five, while some were still further decimated." Writing of the Snowy Owl in Norway, Prof. Collett (1872) informs us that "round about the nest are found mice and lemmings." I suggest these are so placed to serve, as with the Short-eared Owl, as "control food" to deter the older nestlings from committing unnecessary acts of cannibalism.

SUMMARY

Circumstantial evidence indicates that fratricide, in all probability invariably followed by cannibalism, occurs far more frequently among birds of prey than is commonly supposed and, indeed, in a few species is perhaps a normal, rather than an exceptional, practice.

It is suggested that, if properly controlled and chiefly confined to periods of privation (as is apparently the case with *Asio flammeus*), juvenile cannibalism has a definite survival value, and is therefore an important factor in the breeding biology of certain species, particularly in those that lay relatively large clutches of eggs.

Since juvenile cannibalism would be virtually impossible without a considerable difference in the ages of the nestlings, Nature has ensured that difference by "staggering" the hatching dates of the eggs by sometimes as much as two, three or even four days.

The significance of fratricide, so frequently observed in eagles which lay only two eggs, is not clear, since the practice does not appear to be correlated with a dearth of prey.

When food is abundant, a means by which juvenile cannibalism may be controlled is provided in *Asio flammeus* by the deposition of surplus food a few inches from the nest. This practice may also exist in *Nyctea scandiaca*.

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ERRATUM

'The Auk,' 76 (1), p. 107, January, 1959: In the note by J. W. Hardy on a fossil recurvirostrid, the caption to the figure (but not the figure) has the numerals 2 and 3 transposed; *i.e.*, the words "Piece No. 2" should read "Piece No. 3" and *vice versa*.