# GYRFALCON NESTING BEHAVIOR FROM HATCHING TO FLEDGING

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ABSTRACT.—In 1973 two Gyrfalcon pairs were studied in west-central Greenland by time-lapse photography and telescope observations. The role of each sex in brooding and feeding the young was quantified from the film. The female accomplished most of the brooding and feeding. Brooding by the female tapered off, but she did not begin to hunt immediately after brooding ceased. Instead she perched on the cliff, brooding nestlings during times of heat, cold, or precipitation. The male brooded while the female fed herself on food he had delivered to her. Feeding of the young took two forms: (1) active feeding and (2) food delivery. The female actively fed the young until they fledged, but the male began food-delivery visits as soon as they were able to tear up food items by themselves. At one eyrie a cooperative feeding behavior was filmed. Postbrooding visits to the nest were made only to feed the young and were of minimum duration, probably because of the young's aggressiveness. Hunting did not normally take place near the eyrie. The only method of hunting seen was from a perch.—U.S. Fish and Wildlife Research Center, Building 16, Federal Center, Denver, Colorado 80225. Accepted 3 August 1976.

BECAUSE of the Gyrfalcon's (*Falco rusticolus*) northern distribution and early nesting habits, its biology is not so well known as that of most other diurnal raptors (Mattox 1969). Data on some of the Gyrfalcon's nesting behavior are scattered throughout the literature, but no researcher has heretofore made this subject the main object of study. During the summer of 1973 I studied the behavior of two pairs of Gyrfalcons beginning when the eggs hatched and ending when the young left the nest.

### STUDY AREA AND METHODS

The study was conducted in the western inland portion of central Greenland, a region of low arctic tundra with scrubby vegetation and a continental climate with semiarid conditions (Salomonsen 1950).

Two eyries, designated A and B, were studied intensively. Both were situated on cliffs bordering lakes in the same river valley 4.8 km apart.

One super-8-mm time-lapse movie camera was set at each eyrie to monitor behavior periodically. The camera at eyrie A was set to take one frame every 60 sec whereas the camera at eyrie B was set to take one frame every 3 min.

Some limitations of the time-lapse method were overcome by observations with a  $30 \times$  telescope set up about 0.8 km from each eyrie, which also made interpretations of the time-lapse frames easier. A blind was set up 20 m below eyrie A; it was used primarily to film selected behavioral sequences at normal filming speed (18 frames/sec).

The resulting movie film was later analyzed one frame at a time with the aid of a  $6 \times$  lens. As each frame was viewed, the behaviors under investigation were tabulated.

In any behavioral study the investigator must assess the impact of his activities on the behavior of the subject. At eyrie A the adult female returned to the eyrie within 5 min of my leaving the nesting cliff on the first visit. At eyrie B the female also quickly resumed brooding, but the male flew toward the eyrie as though to land but then veered off. This continued for about 15 min until he landed on the eyrie. No other incidents of this nature occurred to indicate nervousness by any of the birds.

Some data were lost during the early morning hours on overcast days owing to insufficient light for proper exposure. The number of frames lost was only 6% of the total exposed.

During the second week of operation the camera at eyrie B failed and could not be repaired; this prevented evaluation of the differences between the two pairs of Gyrfalcons except during the first week. Unless expressly stated all further remarks are concerned with events at eyrie A.

## **RESULTS AND DISCUSSION**

Adult activities at the eyrie.—The activity pattern of the adult Gyrfalcons at the eyrie, as determined from the film analysis, is shown in Table 1. The data are

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Activity category	June					July				
	6-10	11-15	16-20	21-25	26–30	1-5	6–10	11-15	16–20	21-25
Female broods	82	84	77	15	0	0	0	0	0	0
Male broods	11	3	3	2	$+^{2}$	0	0	0	0	0
Female feeds	2	5	5	4	3	2	1	2	1	+
Male feeds or delivers food	+	0	+	+	+	+	+	+	+	+
Adult on eyrie, inattentive	2	2	2	12	11	+	+	+	+	1
No adult on eyrie	3	6	13	67	86	98	99	98	99	99

TABLE 1 ACTIVITY PATTERN OF ADULT GYRFALCONS AT EYRIE A<sup>1</sup>

<sup>1</sup> Values are in percent of total time exclusive of investigator-caused disturbances and frames lost to darkness, and are rounded off <sup>2</sup> A plus sign (+) denotes the occurrence of an activity at a value of less than 0.5%

lumped into 5-day intervals beginning with the day of hatching of the first nestling and ending with the fledging of the second-hatched nestling. The activities were placed into four main categories with the first two categories further subdivided by sex. The main categories are discussed below.

Brooding behavior.—For the purpose of this paper brooding is defined as close sitting or standing over the nestlings by an adult to afford protection from external factors.

As can be seen from Table 1, the female spent almost her entire day at the eyrie brooding during the first 15 days of the nestling period. What data are available for eyrie B suggest that the same was also true there, but that the male at eyrie B assumed a slightly larger percentage of the brooding responsibility.

The nest relief sequence for the Gyrfalcon was the same as Rowan (1922) described for the Merlin (F. columbarius). The male brought food to the cliff and the female flew out to meet him with considerable screaming. She became quiet only after he left or brooded. Usually the male brooded the young while the female ate. After she ate, she picked up the rest of the food item, brought it to the nest, and fed the nestlings. As she approached the eyrie, the brooding male quickly slipped off the nest, seldom actually waiting for her to arrive. He usually left the area, but sometimes perched on the cliff.

Tinbergen (1940) and Enderson et al. (1972) noticed the reluctance of both sexes of European Kestrels (F. tinnunculus) and Peregrine Falcons (F. peregrinus) to be on the nest at the same time; the same reluctance was noticed in the Gyrfalcons. Only eight instances of both sexes on the eyrie together were filmed at eyrie A, with only one instance appearing in more than one consecutive frame. At eyrie B this phenomenon was recorded more often because the two adults there engaged in a cooperative feeding behavior (described below).

Both Nelson (1970) and Enderson et al. (1972) noticed nest worry behavior, i.e. using the beak to "play" with nest material, by Peregrines while brooding or incubating. This behavior was also seen with the Gyrfalcons. Several frames show a brooding adult with its neck outstretched and a twig from the nest held in the beak. The time-lapse film does not show the completion of this behavior, but Nelson (1970) saw Peregrines either drop the sticks or flick them aside.

The cessation of brooding did not occur suddenly. Instead, the young were left unbrooded for increasingly longer periods. The brooding of 15-20-day-old nestlings took place chiefly during times of heat, cold, and precipitation. Brooding behavior began to wane after the nestlings attained their second down coat. The last period of any recorded brooding at eyrie A was for a 2-min period by the male when the young were 19 and 20 days of age.

Female Gyrfalcons leave their young unbrooded at the age of 3 weeks or less and join the males in hunting (White and Cade 1971). At eyrie A the female did not immediately leave the vicinity of the eyrie, but frequently spent time perched within a couple of meters of the nest. Eventually she began to spend increasingly longer periods away from the eyrie, presumably to hunt.

*Feeding behavior.*—Feeding of the young took two forms: (1) active feeding or tearing off small pieces of flesh from a carcass and passing them to the young, and (2) food delivery or passing an entire food item to a nestling. The former was used by both adults when the young were too small to tear morsels from a carcass. After the nestlings developed the strength and coordination to tear up their own food, the male began making food-delivery visits. He began this when the young were 23 and 24 days old, and engaged in active feeding only occasionally after that. The female actively fed the young throughout the entire nestling period, never allowing the young once to feed themselves; observations at eyrie B suggest that this may not be usual behavior.

Feedings were recorded for every hour of the day, with a maximum occurring around 1600 and a minimum at midnight. There was little regularity or predictability to feedings; any periodicity would be linked to hunting success and prey activity cycles.

The first recorded feeding of the young took place on the first and second day of age for the two nestlings. In contrast, Enderson et al. (1972) recorded feedings within 4 to 8 hours of hatching for Peregrines.

Before both nestlings fledged, the adults appeared to be delivering food to the nest rather than to the nestlings. Even if the nestlings were standing only a few meters away from the nest on nearby ledges, screaming and flapping their wings, the adults landed on the nest. Comparable behavior is known for the European Kestrel, Hobby (*F. subbuteo*), and Peregrine Falcon (Tinbergen 1940, 1968; Nelson 1970). After the first nestling fledged, the adults still delivered food to the nest rather than to the fledgling. Hence the first-fledged young was forced to return to the nest to be fed 8 times after fledging and before its nest-mate fledged 2 days later.

Postbrooding visits to the eyrie by the adults were made only to feed the young and were of minimal duration, particularly those of the male. The mean duration of 3 timed food-delivery visits made by the male was only 9.3 seconds. With an exposure rate of 1 frame/60 sec, many of these short visits would not have been recorded by the time-lapse method. The visits could be inferred, however, by typical actions of the young. The nestlings flapped their wings and screamed whenever an adult appeared in view, and the nestling that got the food item would cover and guard it from its sibling. An "apparent" food-delivery visit was recorded if either or both of these behaviors was seen on the film. All "apparent" food deliveries were attributed to the male as the female actively fed the young at least until they fledged.

The reason for the shortness of the food-delivery visits is evidently the aggressiveness of the hungry young toward their parents. On one of the male's visits, filmed at 18 frames/sec, a nestling seized the food item and carried it to a corner of the eyrie to eat. The other nestling continued to beg from the male and went so far as to grab the male's crop with its foot. The male wrenched free of its grip and flew off. Such aggression has been noticed in other raptor species (Tinbergen 1968, Ellis 1973).

At eyrie B the film shows a feeding behavior not seen at eyrie A, nor reported in

any of the Gyrfalcon literature I reviewed. Several of the frames show the adult female brooding, followed by frames without an adult on the nest. Next the male is seen brooding, and the female then appears on the nest with a food item. The inference is that the male delivered food to the female off the nest and then brooded as she ate, a sequence seen many times at eyrie A. However in this case the male did not leave the eyrie immediately upon return of the female. The female was then seen standing on the food item, tearing a tidbit from the carcass, and giving it to the male. The male then fed the tidbit to the nestlings. The adult male usually ended this cooperative feeding behavior by leaving the eyrie and the female finished feeding the young.

The reluctance of the two adults at eyrie A to be on the nest together was discussed above; the eyrie B adults were somewhat an exception. They were filmed together 16 times (243 min total) while the adults at eyrie A were on the nest simultaneously only 5 times (6 min total) during the first week of brooding.

All excess food items were removed from the nest by the adults until the young were well enough developed to feed themselves. The adults picked up the food in their beaks, lept into the air, and then brought their feet forward to transfer the items to the feet.

Food items removed from the eyrie were generally cached. During the early nestling phase, most food items were large enough for the adults and nestlings to eat a meal and still have enough left to cache. In caching the remains, the female was seen to make several efforts to place the food items behind tufts of grass, in a probable attempt at concealment. One general part of the nesting cliff was always used for caching, and three or four different specific sites were used. Not all cached items were retrieved. One cached Oldsquaw (*Clangula hyemalis*) was left untouched and became infested with maggots. The male was never seen to cache food, which contrasts with the observations by Nelson (1970) of male Peregrines using caches.

Adult on eyrie, inattentive.—Behavior observed on the film was placed in this category when an adult was perched near the nest (within 2 m), but was not brooding or feeding the young. During the first 15 days of brooding (6–20 June at eyrie A) this behavior usually occurred in transition between other activities. For example, the female often stopped brooding and stood on the edge of the nest when she saw the male approaching the cliff with food. The increase of inattentive behavior at the eyrie during the 16th through the 25th day after hatching (21–30 June at eyrie A) resulted from the female's habit of perching near the eyrie during the waning of brooding behavior, as discussed above.

No adult on the eyrie.—The absence of the adults from eyrie A greatly increased after the 15th day following hatching (20 June). After the 25th day following hatching (30 June), the adults spent less than 3% of the day at the eyrie (Table 1). My visits to the nest during the last half of the study period usually did not bring on defensive reactions by the adults, suggesting that they were not within sight of the eyrie.

Hunting behavior.—It has been stated that raptors do not hunt near their nests (Meinertzhagen 1959). At the beginning of the study I found evidence of four ptarmigan kills near the eyrie, although these may have been killed before nesting began. Once, while I watched from the blind, the male flew on a straight line from the nesting cliff to a hillside and unsuccessfully chased some undiscernible prey on foot. Although these examples suggest that hunting may sometimes occur near the nest, most hunting probably does not. It was usually possible to visit the eyrie after brooding ceased without seeing either adult (both were presumably away from the eyrie hunting). The three other instances of hunting that I observed took place 1.6 km or more from the eyrie; they were all unsuccessful attacks launched from perches.

*Flight behavior.*—The Gyrfalcons used wind and terrain to reduce the energy expenditure of flight by using orographic lift (upcurrents of air deflected by hills and cliffs). The most common method was to quarter back and forth in front of the nesting cliff on windy days, gaining altitude and gliding to a destination. When flying away from the eyrie, they used the updrafts from a cliff across the lake to gain altitude.

*Gyrfalcon pair conflicts*.—Only one instance of possible conflict between pairs A and B was witnessed. During a filming of the female feeding the young at eyrie A, a Gyrfalcon flew into the nest and apparently tried to rob the female of her prey. She reacted by trying to grab the intruder with her foot and missed; she then cackled at the strange falcon but made no attempt to pursue it. The intruder was a white falcon and therefore not her mate, which was gray. If Kishchinskii's (1957) estimate of 10–15 km for the diameter of the Gyrfalcon's hunting area is correct, then eyries A and B are within the hunting range of each other and the intruder could have been from eyrie B. The next nearest known active Gyrfalcon eyrie was 19 km distant.

Interspecific behavior.—The Peregrine Falcon is a breeding summer resident on the study area and may compete with Gyrfalcons for some resources. An adult female Peregrine roosted for a "night" on a cliff 0.6 km from eyrie B and cackled defensively when disturbed. She may have been the female of a pair that attempted to nest halfway between the two Gyrfalcon eyries.

Two Gyrfalcon-Peregrine conflicts were seen near eyrie A. An immature Peregrine "buzzed" the adult male Gyrfalcon while he was perched on the nesting cliff. The Gyrfalcon was visibly surprised by the attack, as evidenced by the rapid opening of his wings, but he remained on the cliff while the Peregrine soared away. On the other occasion, an adult Peregrine traded dives with the female Gyrfalcon.

The relationship between ravens and Gyrfalcons is seemingly paradoxical. Some Gyrfalcons may be dominated and mobbed by ravens (Meinertzhagen 1959), the two may act as commensals (White and Cade 1971), or ravens may be prey for the falcons. The literature reveals that ravens do not constitute a substantial part of the Gyrfalcon's diet, but cases of ravens killed by the falcons are reported by Cade (1960), Brüll (in Cade 1960), and Roseneau (1972); remains of one freshly killed and eaten raven were found on eyrie A.

The eyrie B adults consistently ignored the squawking ravens that successfully nested only 50 m away from them, even when the ravens flew directly beneath or over the eyrie. This is in contrast to the reaction of the female at eyrie A, which quickly stood up to protest loudly the intrusion of a raven flying beneath her eyrie, and in contrast to this pair's predation on a raven.

The variability of the Gyrfalcon-raven relationship is probably owing to the difference in the "psychological" character of individual birds, some Gyrfalcon and raven pairs being more compatible than others.

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