

OBSERVATIONS ON GYRFALCONS (*FALCO RUSTICOLUS*) BREEDING NEAR LAKE MYVATN, ICELAND, 1967

by

Nick Woodin

Star Route

Ausable Forks, New York 12912

Introduction

This paper is based on observations made between 2 March and 23 August 1967 in the Lake Myvatn region of northeastern Iceland and during a brief stay (24 to 28 August) on the island of Hrisey in the Eyjafjörður of north central Iceland. I was supported during my stay in Iceland by a Fulbright Fellowship.

Iceland is one of the few places in the world where it is possible to study relatively abundant Gyrfalcon populations from accessible and permanent human habitations. One of the reasons I have written up a single season's work at such length is in the hope that some other student will take up the study where I left it.

For advice and assistance I am indebted to Finnur Gudmundsson and Arnthor Gardarsson. Dr. Gudmundsson suggested the project, and without his and Arnthor's help, it would have come to much less. I am grateful to the staff of the Museum of Natural History, Reykjavik, for their kindness to a foreigner, and to Professor Tom Cade for inspiration and advice.

The Region

Lake Myvatn is located at approximately 65½° north latitude in the northern part of the arid, young-volcanic zone of Iceland. The lake, 277 m above sea level, is about 55 km inland from the north coast. Characteristics of the young-volcanic zone are relatively low precipitation and much dry moorland, with a vegetation chiefly of low-growing heaths (*Ericaceae*), creeping willows (*Salicaceae*), dwarf birch (*Betula nana*), and crowberries (*Empetrum nigrum* agg.) (Gudmundsson 1960). The Myvatn basin also contains extensive brushwoods of birch (*Betula pubescens*) and large wastes of poorly vegetated sand, gravel, or lava. South of the lake lie marshes with clumps of willow. The lake environs are excellent habitat for waterfowl. Bengtson (1971) estimates that between May and September the area contains rarely fewer than 25,000 ducks. Shorebirds, including Redshank (*Tringa totanus*), Golden Plover (*Charadrius apricarius*), Snipe (*Gallinago gallinago*), Dunlin (*Calidris alpina*), and Whimbrel (*Numenius phaeopus*), also breed about the lake. There is at least one colony of the Blackheaded Gull (*Larus ridibundus*). The region is the center of the distribution of the Icelandic Rock Ptarmigan (*Lagopus mutus islandorum*), the only gallinaceous bird in Iceland (Gudmundsson 1960). All these birds are potential prey for Gyrfalcons. Mammals are not common but include the Arctic fox (*Alopex lagopus*), long-tailed field mouse (*Apodemus sylvaticus*), probably the mink (*Mustela vison*), and the brown rat (*Rattus norvegicus*).

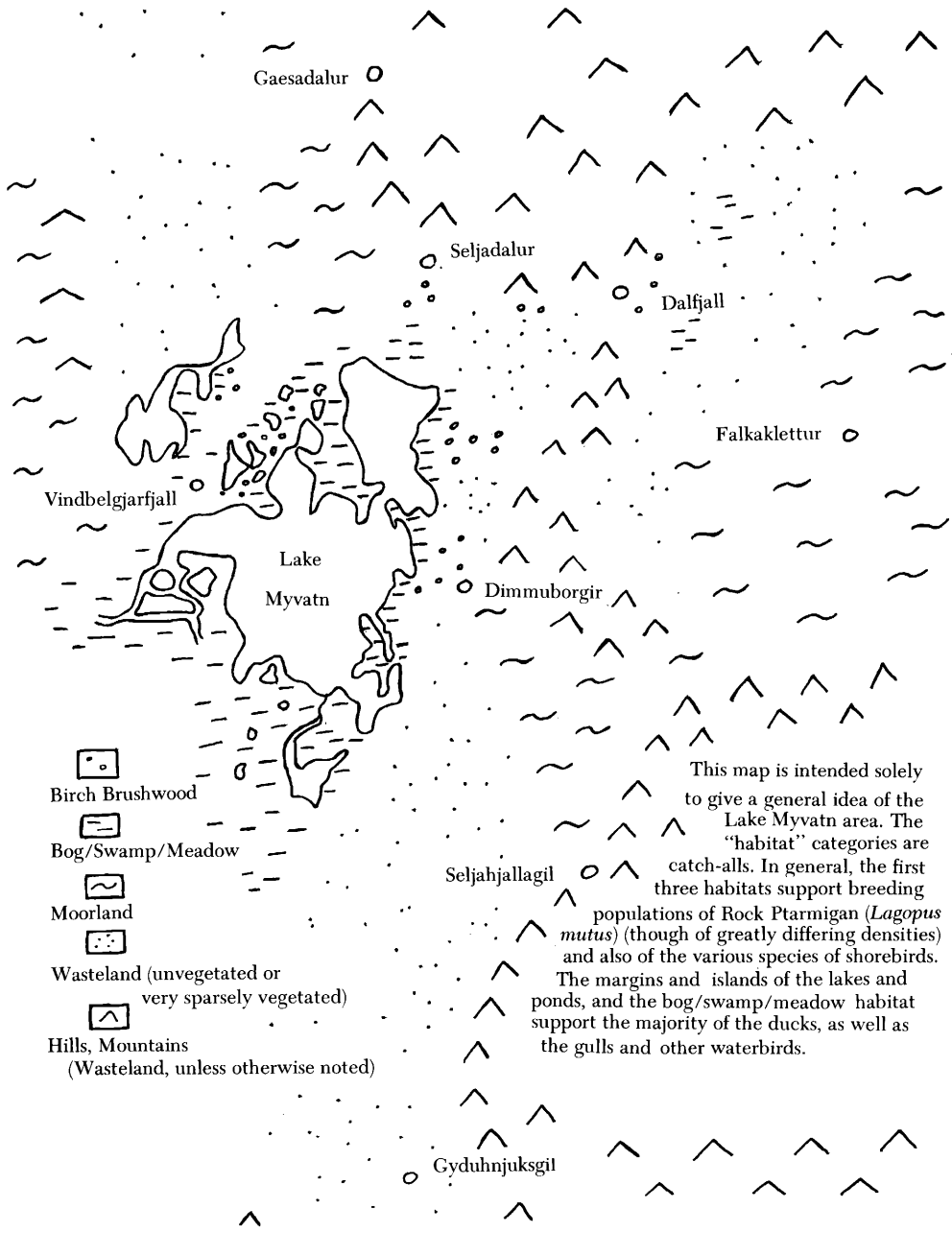
Lake Myvatn lies in a basin more or less enclosed by slopes, low hills, and mountains. What I have called the Myvatn eyries are located in the canyons or on the exposed faces of the nearer hills and slopes (fig. 1). They tend to be within 10 km of the lake and 100 to 200 m above it. By way of contrast, the highest mountains near the lake range from 500 to 900 m above it, at distances of 12 to 15 km. The most geologically isolated eyrie is Falkaklettur, which is located beyond the eastern hills on a high rock in the middle of an extensive, well-vegetated lava field.

The farmers of the Myvatn basin raise sheep and cattle. Livestock graze outside for part of the year. Hay is raised for winter feed, for the most part within a few hundred meters of the lakeshore. Sheep have exerted an enormous influence on the Icelandic landscape, but other than that man's effect on the wildlife of the Myvatn basin has probably been relatively little. In 1967 farmers still supplemented their incomes by netting Arctic char (*Salvalinus alpina*), and shooting Rock Ptarmigan and Grey-lag Geese (*Anser anser*), but their harvests were not excessive. The number of people in the basin is small. But as of this writing "modern life" has arrived at Lake Myvatn. The bottom mud of the northern, shallower basin of the lake is being mined to produce diatomaceous earth. This activity will force development of reliable year-round road communications and a year-round port on the Greenland Sea. The lake is located within a geothermal area that is a potential source of electric power. The next decades may well involve further industrial disturbances of the Myvatn landscape, with unforeseeable effects on its wildlife populations, including its population of Gyrfalcons.

Purpose and Methods

I stayed with the family of Snaebjorn Petersson in Reynihlid (fig. 2). The chief purpose of my stay at Myvatn was to determine whether the Gyrfalcons' food habits showed any change over the breeding season. F.

Figure 1 Resident Gyrfalcon Pairs and Habitats at Lake Myvatn, 1967



This map is intended solely to give a general idea of the Lake Myvatn area. The "habitat" categories are catch-alls. In general, the first three habitats support breeding populations of Rock Ptarmigan (*Lagopus mutus*) (though of greatly differing densities) and also of the various species of shorebirds. The margins and islands of the lakes and ponds, and the bog/swamp/meadow habitat support the majority of the ducks, as well as the gulls and other waterbirds.

Figure 2 Eyrie Areas of Gyrfalcons at Lake Myvatn

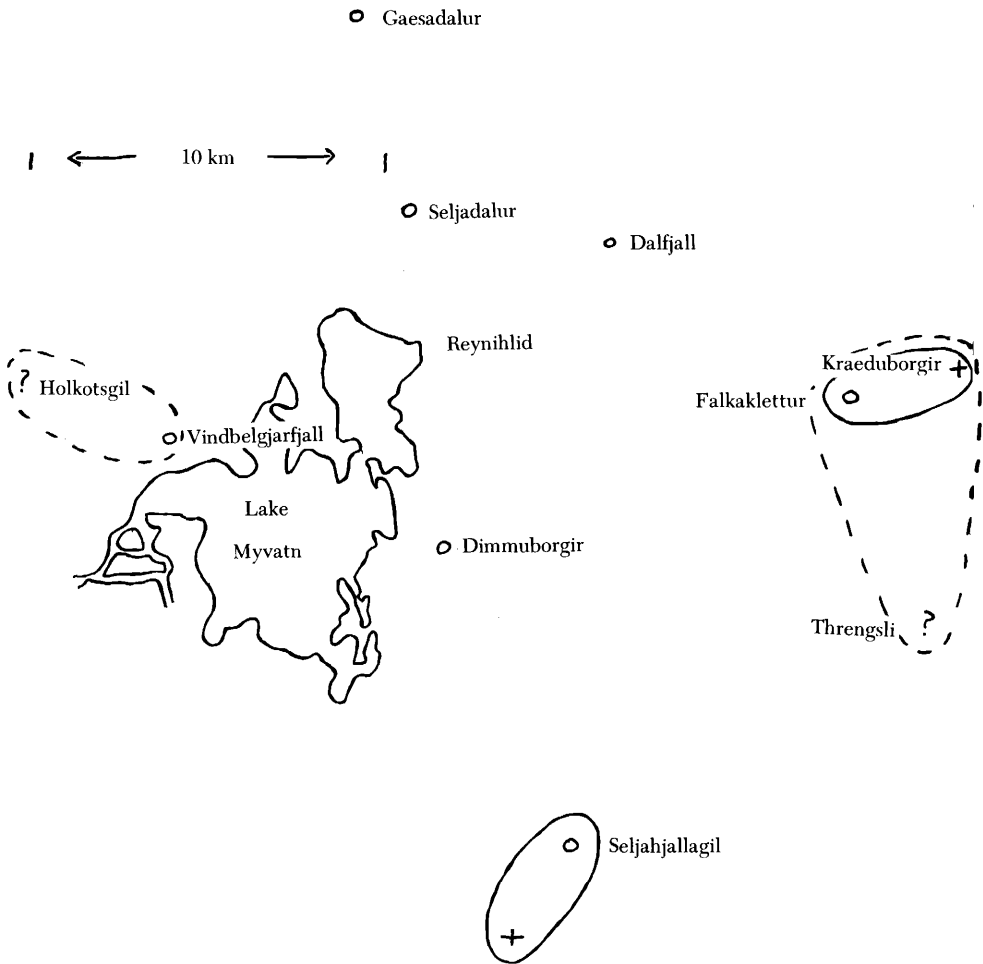


Figure 2 summarizes my interpretation of eyrie areas at Myvatn. Occupied areas are marked by a circle, former ones by a cross. Alternate areas are joined by a solid line. Areas which I suspect function primarily as alternate areas, but which are more than 3 km away from each other, are joined by a dotted line.

● Gyduhnjuksgil

Gudmundsson and A. Gardarsson had observed that Gyrfalcon predation on the Rock Ptarmigan on Hrisey virtually ceased the first week in June. They wanted to know if a similar shift away from ptarmigan as food occurred at the eyrie. At the same time I was to fit in whatever other observations on Gyrfalcons I could.

Transportation was by ski, foot, and bicycle. Use of the bicycle became possible in mid-May. Until then I observed the closest of the eyries: Seljadalur, Dimmuborgir, and Dalfjall (fig. 2). Seljadalur was just a 45-min. ski from the house. When the Seljadalur pair failed to lay eggs, I focused on Dimmuborgir, with periodic visits to the other eyries. A. Gardarsson had shown me the locations of most of the eyries before I left Reykjavik.

One of my chief concerns was the extent to which my presence might influence the Gyrfalcons' behavior. Their reaction to me varied as the season progressed. They became more aggressive after egg-hatching. Before egg-laying, adults were rather shy, and it was difficult to assess one's effect. I tried to remain as inconspicuous as possible. My equipment included 10 by 40 binoculars and a 30-power telescope. I did not use a blind. The positions from which I watched the eyries were not always good. Rarely could I command a view of both the eyrie and the approaches to it. At Seljadalur I generally picked a spot on the canyon floor, 250 m or more from the nearest perching place. This position afforded a restricted horizon but a good view of the interior of the canyon. A few times I observed from one of the ridges that bordered the canyon, where I had an excellent long view in all directions but was unable to see most of the perching places in the canyon itself.

When I began regular observations at Dimmuborgir, the pair would tolerate me within 250–300 m as long as I remained down near the valley floor. When I took a more commanding position on a slope, about 300 m from the nest ledge, they began periodic fly-overs or otherwise indicated their agitation. I finally adopted a position on the valley floor about 250 m from the nest ledge, which gave me a good view of the nest and of the surroundings for a few hundred meters in each direction. My concern was to tell the direction from which the mates were arriving, but this was rarely possible.

At Seljahjallagil I took a position that let me view the nest ledge, the inner walls of the canyon, and the sandy waste and distant lake beyond. Thus I was able to observe in some cases the direction of arrival of the adults with prey.

Falkaklettur was probably the best eyrie to observe. It was situated on a lava rock in the middle of a fairly flat lava field. I could keep both the rock and approaches to it in view. After egg-hatching, however, the female at Falkaklettur would not tolerate me within 500 m of the nest unless I remained completely hidden.

Early in the season I went out whenever weather allowed, generally for short periods of 4 to 5 hours. In May and June my observations focused on Dimmuborgir, and I spent 4 to 8 hours a day watching the eyrie 4 or 5 days a week. In July and August I alternated longer trips to the distant eyries with shorter trips nearer home. Long trips involved 2 to 3 hours of travel to the eyrie, 4 to 8 hours of observation there and a similar amount of travel back. I spent about 700 hours in the field, 250 to 300 of them in direct observation of Gyrfalcons.

The Eyries

Brown and Amadon (1968) define *home range* and *nesting territory* as they apply to diurnal raptors. The *home range* is the entire area used by a breeding pair or solitary individual. The *nesting territory* is the area about the nest that is defended. In some cases the two coincide, but often the "outer" parts of the home range (which usually comprise the hunting territories) are not vigorously defended and may even be shared. Cade (1960) uses a model of the latter sort to describe the home ranges of the Peregrine (*Falco peregrinus*) along Alaskan rivers. His diagram of a typical home range consists of three concentric circles of increasing diameter centered on the eyrie. The inner circle is always defended against other Peregrines. Inside the second circle intruders are sometimes attacked, and in the outer circle other Peregrines are attacked only over food items or favorite perches. The diameter of the inner circle varies from 100 m to 1.6 km, and that of the outer circle is a little more than 3.2 km. The outer circles of adjoining home ranges overlap. The notion of a large home range, vigorously defended for a small radius about the nest ledge, and loosely defended or even "shared" at greater distances from the nest, fits my observations of Gyrfalcon behavior at Myvatn.

Beebe (1960) uses the term *eyrie area* to refer to the entire area in which, year after year, different nest ledges are occupied by one pair of Peregrines. Gyrfalcons, like Peregrines, tend to use alternate nest ledges on a given cliff or in a given canyon (Hagen 1952). However, at Myvatn two of the home ranges contained two distinct eyrie areas, about 3 km apart, which appeared to function as alternate areas for the same pair. In this case, it seems that the space between these areas should not be classified with them. Rather one might refer to them as alternate eyrie areas. At Dalfjall, on the other hand, several nest ledges were scattered along approximately 3 km of a mountain fault.

1. *Dimmuborgir*. The eyrie in 1967 was in an old nest of the Common Raven (*Corvus corax*) on a ledge in a lava butte. The ledge faced west and was completely overhung. One could walk up to it. Another nest report-

edly exists in Dimmuborgir, but I did not search for it. Dimmuborgir (Dusky Castles) is a lava depression, roughly circular, between 1 and 2 km in diameter. A small central plateau is surrounded by a confusing maze of lava buttes, pinnacles, and valleys. A pair each of ravens and Merlins (*Falco columbarius*) nested near the part of the depression occupied by the Gyrfalcons.

The pair hatched 4 young from 4 eggs. Three of the young disappeared within a week, probably because of my, or others', interference. The fourth young died of unknown causes when virtually fully fledged. Dimmuborgir is a national park. One can drive to it, and after the first of June human disturbance is common. Because of its accessibility, it was also the eyrie I watched most frequently in May and June.

2. *Dalfjall*. The eyrie area at Dalfjall consists of approximately 3 km of a fault that cuts through a mountain ridge. Several inaccessible rocks and faces showed apparent Gyrfalcons use. The large cliffs overlooking the plain to the east showed much use, held at least one former nest ledge, and seemed to be the center of activity for the nonbreeding pair in 1967. The previous year's nest had been an old raven nest further north along the fault. This nest was in a low face in a pothole just large enough to hold it. About 1 m below the nest was a grassy ledge to which one could walk. A pair of ravens nested on the northern extremity of the fault in 1967. Copulation and one attempted food transfer were observed in the Gyrfalcons.

3. *Seljadalur*. The eyrie area centers on the east cliffs of a narrow canyon which opens out into a little plain below. The cliffs are about midway along the canyon, where it narrows before bending abruptly 90° and ending in a steep slope. The Gyrfalcons used several ledges and rocks on the western side of the canyon in late winter and early spring, including an outcrop below the canyon proper. The only site that seemed to show signs of previous nesting was an old raven nest on the east cliff. In April a pair of ravens began building a new nest near the old one. After egg-laying by the ravens, a series of spectacular fights occurred between the ravens and the Gyrfalcons, which finally resulted in the ravens remaining where they were and the Gyrfalcons establishing control over a section of the cliffs with what appeared to be a suitable nest ledge above and up the canyon from the ravens. However, the Gyrfalcons did not lay eggs. Their ledge had fresh prey pluckings and molted Gyrfalcons feathers on 20 July.

Whether the Seljadalur area is a separate eyrie area, or an alternate one (to either Dalfjall or Gaesadular, most likely the latter) is not clear. Three factors make me question its separateness: it is rather close (about 5.5 km) to both Gaesadalur and Dalfjall; it is between Gaesadalur and Lake Myvatn; and vegetative signs seem to indicate that Gaesadalur and Dalfjall have been more consistently occupied.

4. *Vindbelgjarfjall*. The eyrie area centers on cliffs along the southeast side of "Windbag Mountain," a steep hill rising about 250 m from a marshy shrubland dotted with ponds. A pair of ravens nested in 1967 on the western end of the cliffs and a pair of Merlins on the eastern end. At least one ledge in the central and highest section seemed to show signs of former Gyrfalcons occupation, and this area also comprised the center of activity for the nonnesting pair in 1967.

Breeding activity extended only through copulation. On 26 April 2 Gyrfalcons in juvenile plumage were "escorted" away from the cliffs by the adults.

Between 4 and 5 km away over the moor is a low, rocky upjut that forms part of a bowl (Holkotsgil) in the side of the Laxa River Valley. There I saw Gyrfalcons several times and found prey remains and molted feathers. The upjut contains a raven nest, but as far as I could tell Holkotsgil has not been used by Gyrfalcons for breeding. I think the Gyrfalcons I saw there were from Vindbelgjarfjall.

5. *Falkaklettur*. The eyrie area centers on a lava cone that rises about 6 m above a grassy base on the Burfellshraun lava field. The Burfellshraun is well-vegetated and supports breeding populations of ptarmigan and shorebirds. The eyrie was in a north-facing hole, about 0.5 by 0.3 m, just below the top of the cone. A crevice on the west face formed a narrow ledge through an accumulation of prey remains and pellets. It apparently served only as a perch. A lava rock to the south showed signs of occupation by Merlins, but none nested there in 1967.

About 3 km to the east is a group of upjuts (Kraeduborgir) with ledges that showed use by Gyrfalcons. According to local farmers, this is an alternate site for Falkaklettur. I also found a site used by Gyrfalcons in Threngsli, between 6 and 7 km south of Falkaklettur. Here a small pothole or cave near the top of the cliff had a mound of pellets, another of excrement (mutes), some old prey remains, and several recently molted Gyrfalcons feathers. About 10 m around the cliff in a similar pocket was a new raven nest and about 15 m further on an older one. The male at Falkaklettur was very shy of his mate, and possibly he used the first cave as a perch. However, because of its distance from Falkaklettur it could have been a separate eyrie. If so, it was not successful in 1967. I found it on 7 August, 3 weeks after young fledged at Falkaklettur. As I climbed about the cliff, 4 Merlins swooped and tumbled overhead.

6. *Seljahjallagil*. The eyrie area consists of the upper part of a narrow canyon (gil) that cuts into the upland bordering the lake basin to the east. Two ledges showed use, but the only one I could identify as an eyrie was that used in 1967. The slightly overhung ledge measured about 1 m by 0.3 m and was located on the south

side of the canyon, with a grassy and stony slope below. It showed previous use. Four young were fledged in 1967. The lower part of the gil contained a volcanic crater, several of whose inner ledges showed signs of use by Merlins. One held an eyrie, where 3 young were fledged.

Approximately 3 km south of the Gyrfalcon eyrie are two smaller canyons that open together into the plain toward the lake, and immediately south of them are two bowls in the side of the upland, which has here become a mountain (Blafjall). The more southerly canyon had a possible former eyrie site, and the northern hollow at least two. The further hollow had one very suspiciously green ledge. Because of the area's closeness to Seljahjallagil I thought it an alternate area. An old raven nest in the southern part of Threngslaborgir could also serve as an alternate site. Threngslaborgir is very confusing, and I could not find the raven nest again, but it was also about 3 km from the eyrie at Seljahjallagil.

7. *Gaesadalur*. I found Gaesadalur on 17 August. The eyrie was on one of the ledges on the south side of the valley, near where it opens into the plain Randir. The ledge was about 8 m above the valley floor, inaccessible without a rope, and was apparently a much-used site, judging from the amount of orange lichen, the thickness of the moss on the cliff, and the vigor of the *Salix herbacea* on the slope below. Chunks of moss had fallen off the face, out of which I picked ptarmigan bones dyed a dark red. Juvenile down on a lower ledge and along the shore of the pond, where there were also three recently picked-over duck carcasses, indicated a brood had fledged. This face was the only eyrie site I found in the canyon, but the upland between Gaesadalur and Seljadalur contains many likely-looking places.

8. *Gyduhnjuksgil*. I visited Gyduhnjuksgil on 12 August. The gil opens out into a dry wash in a stony plain that rises slowly between the two mountains at the southern end of the lake. The area that contained the former eyrie sites was the lower 150 m of the gil. About 1 km up the gil I found a rock on the west side that looked like a Merlin site. The Gyrfalcon eyrie was in a raven nest on a rock face that stood out into the gil itself. The nest was inaccessible without rope. There was another raven nest on a ledge below. A face near the entrance to the wash had two possible former eyrie ledges, overgrown with tall grass. Juvenile down on a perch at the entrance to the gil and fresh prey remains below the nest indicated that a brood had fledged.

9. *Hrossaborg*. Hrossaborg is not a Myvatn eyrie. The eyrie area consists of a crater whose walls make a natural shelter for the level ground inside: thus, perhaps, its name—the horses' castle. The crater is located just south of the road across the Burfellshraun, about 3 km from the Jokulsa-a-Fjollum River, and 17 km from Falkaklettur. It has four main cliffs, all of them on the outside. On 19 June, I found nothing on the northeast cliff, a pair of brooding ravens on the northwest cliff, a partly collapsed old raven nest high up on the southwest cliff, and a pair of Gyrfalcons with 4 downy young in a raven nest on the southeast cliff. The nest was tucked into one of a series of long, slanting shelves, about 3.5 m above a gravel slope. It faced east and was completely overhung.

On 19 June the nest contained 4 large downy young. However, several things bothered me about the adults. During the 3 hours I watched the nest, the male brought prey once. The female took it, fed herself, and did not feed the young. I saw this happen very few times during my stay at Myvatn. It might have been a response to my presence. Second, the color of the female's plumage was midway between that of an adult and a year-old juvenile. I was not sure her feet were yellow. Finally, during my approach to the nest the male was much more aggressive than the female. Perhaps the female was a young bird breeding for the first time.

Between 19 and 24 June a photographer set a blind about 50 m from the nest. I dismantled it when I visited the eyrie on 24 June. On this date, 1 young had disappeared, 1 was apparently dying, and the other 2 were somewhat lethargic. Neither adult appeared during the hour I spent there. On 26 June the remaining 3 young were dead. Neither adult was present. Apparently the nest was abandoned because of the blind, and the young then starved.

Behavior during the Breeding Season

Pre-laying. A central question in the study of wild Gyrfalcons has been whether they winter on the breeding grounds. Platt (1976), working in the western Canadian Arctic, found Gyrfalcons in the vicinity of their nests in January and February. Bengtson (unpubl. ms.) reports Gyrfalcons about Lake Myvatn in December. Platt (1976) presents data that suggest that, at least in the higher latitudes of North America, the adult males may remain on the breeding grounds over the winter while the juveniles move south. Platt found potential prey, Willow Ptarmigan (*Lagopus lagopus*), relatively abundant in January and February. The major difficulty for predators at high latitudes is probably the short length of day (3 hours in mid-January for Platt's plot) during which to obtain

prey. Casual observations near Reykjavik, southern Iceland, during the winter of 1966–1967 indicate that at least some of the juvenile Gyrfalcons remain on the island. They seem to suffer a heavy late autumn and early winter mortality from starvation and disease (probably aspergillosis). Platt (1976) suggests that juvenile Gyrfalcons, lacking hunting skills, tend to pursue ground-dwelling prey, such as lemmings, and disperse to areas where such prey is more abundant for their first winter. In fact, Gyrfalcons may learn to hunt on essentially ground-dwelling prey. The juvenile Gyrfalcons I watched in late August in northern Iceland were catching juvenile ptarmigan on the ground. The young Gyrfalcons would attempt to grab the young ptarmigan while flying over them and, if this maneuver failed, would land and pursue them on the ground. One often sees juvenile Gyrfalcons at the Reykjavik city dump in the autumn, where they pursue brown rats (*Rattus norvegicus*).

Whether Gyrfalcons spend the entire year on their home ranges depends on the availability of prey. The Rock Ptarmigan, which forms the chief prey of at least the inland populations of Icelandic Gyrfalcons, spends the autumn and winter grouped in nomadic flocks, which perform a limited seasonal migration. In the autumn after acquiring white winter plumage, ptarmigan move from their breeding grounds to higher elevations where snow has already fallen. They then follow the snow line as it moves down the mountains. Thus, depending on the other prey species available to a given population of Gyrfalcons, one might expect a general autumn dispersal of Gyrfalcons (perhaps still in family groups) in pursuit of ptarmigan, followed by a return, perhaps of the adults only, to the breeding grounds in December, when snow cover is more general and the ptarmigan more spread out. The return would depend on suitable winter cover for ptarmigan being available in the home ranges of the Gyrfalcons. Suitable winter cover for ptarmigan in Iceland consists primarily of brushwoods of birch (*Betula pubescens*). Since Gyrfalcons breed so early and presumably need some weeks of socialization prior to egg-laying, it may be that one of the prerequisites of a home range is a certain amount of birch brushwood.

In March, when I arrived at Myvatn, Gyrfalcons were paired. At Dimmuborgir the nest was being used for a perch. On 10 March a cup had been scraped. Upon my approach this day, the single bird did not leave the area directly, but circled several times around the lava butte containing the nest before disappearing.

Prior to egg-laying, all the falcons spent a good deal of time perching, singly or together, in the immediate vicinity of the former nest sites. They also roosted near old nests at night. The Seljadalur pair had perches both in the immediate vicinity and scattered about the general area. The more distant perches were within 1.5 km of the canyon, mostly to the west and south. In April, after copulation began, they perched together for hours in the afternoon and evening, copulating every hour or two, and going from one perch to another. It was not clear if the birds at Dimmuborgir and Dalfjall made use of such distant perches. Hunting at this time still appeared to be a solitary activity.

Ptarmigan were common in March and the beginning of April both in the birch scrub on Dalfjall and at Seljadalur. Judging by remains found then and later during the thaw, they had been taken by the Gyrfalcons at both places. Thus it seems that the free or safe area for prey about the eyrie, which some observers have reported (Dementiev 1960), does not exist prior to egg-laying.

On 4 April I first observed copulation (at Dimmuborgir). It was accompanied by sev-

eral vocalizations. Since the calls I recorded agree well with the repertoire described by Wrege and Cade (1977), and that summarized by Cramp and Simmons (1980) for the various events in the breeding cycle, I will not enumerate them here. I have made my classification of calls in this paper fit theirs.

On 4 April preening movements by the female and many soft calls immediately preceded mounting by the male. During copulation the female bowed her head almost to the ground, while the male balanced on her back, slowly moving his wings. After copulation the male left the area and had not reappeared by the time I left, an hour and 45 min later. Such disappearances at Dimmuborgir seemed the rule only for the first few days. They also occurred from time to time at Seljadalur, and there was some indication that they were associated with hunting by the male. On 8 April copulation in Dimmuborgir was accompanied by a chittering call.

Copulation at Seljadalur sometimes, but not always, involved more elaborate precopulatory behavior. The most elaborate of such behaviors that I observed occurred on 5 April and consisted mostly of preening movements. The mates faced each other about 8 m apart on a snow-covered slope. First one bird and then the other took the initiative at preening. The movements included lifting and preening under the wings; bending the head back while elevating the tail, as though to touch the beak to preen gland; scratching under the chin; and lowering the head while bobbing the tail. One of the last in the sequence, done only by the female, was a bending of the tail sideways, while reaching back under it with the head. Such preening episodes occupied 20 min, when the male took off and mounted the female, as usual, from the wing. Billing was part of the copulatory behavior at Dimmuborgir but not at Seljadalur. I also observed mantling of the mates to each other during an afternoon of perching and copulation when the mates were perched facing each other, less than a meter apart.

Flight display did not seem highly developed among these Gyrfalcons. The bulk of their courtship behavior consisted of perching near each other. However, normal flight patterns seemed to become more elaborate, or were executed with more speed or grace during courtship. I twice saw mutual gliding during courtship. At Seljadalur this behavior followed copulation. The mates soared above the canyon and then descended in long glides, so that they crossed and recrossed each other's paths. One dove from a short distance at the other, which I think turned on its back to meet it, and finally one followed the other in a long swoop (I heard a burst of calls at this point) that carried them out of sight.

Later in the season, from time to time I saw one or both of the mates at Dimmuborgir perform a flight display above the eyrie; the bird would either soar with the eyrie as a center below it or glide at a lower altitude in a series of circles or arcs that took it back and forth over an area of 200 to 300 m radius. Twice during the fourth week of incubation at Dimmuborgir, I saw one of the mates (once the female, once the male) go into a stoop in the eyrie area, once right before the eyrie ledge and once a little way off. In both cases the stoop was associated with a flight display above the eyrie. Finally, on 11 April, I saw a single Gyrfalcon make a morning flight at Seljadalur. That morning I had been watching the canyon since 0445. Sun first shone in at 0700. At 0800 a gyrfalcon appeared on the wing, swooped down across the valley, then up and back and disappeared from sight. In less than a minute, the falcon came around the face again, made a feint down, falling and twisting, then swooped twice way up, sliding down the rising air currents above the top of the canyon. Finally it came motionless into the wind, high

up, and then disappeared in a long circle. A few minutes later I spotted a gyr perched on a face. It preened until 0830, and was still perched in the sun when I left at 0900.

Of the 4 pairs of gyrs I was observing in April only one pair (Dimmuborgir) laid eggs. I observed copulation in 3 of the 4 and suspect it occurred in all 4 pairs. At Dimmuborgir, egg-laying essentially marked the end of copulation. Egg-laying ended between 18 and 19 April. I observed only two copulations after this, on 19 and 24 April. One occurred after I had disturbed the brooding bird (the male), and the other seemed to be a substitute for the male's failure to bring food. The last copulation I observed at the other eyries was at Seljadalur on 20 April. On this day the birds spent most of my observation period (1000 to 1900) perching side by side on different posts within 1–1.5 km of the canyon. Copulation occurred twice (once in the canyon, once about a km away). All the pairs seemed to use their eyrie areas as a home base at least into June.

Egg-Laying and Incubation. Egg-laying occurred about the middle of April. As nearly as I could judge from the development of young in other eyries, the Dimmuborgir pair laid eggs near the middle of a two-week laying period for the region. Egg-laying thus coincided with the arrival of cock ptarmigan on the breeding grounds and also (but I think less significantly) with the arrival of the first migrant waterfowl. At Dimmuborgir egg-laying also marked the start of fairly regular food transfers from male to female. It was not clear when food transferring began or whether it was regular before egg-laying. An instance of food transferring occurred near Dimmuborgir on 8 April, and I observed an apparently unsuccessful attempt at food transferring at Dalfjall on 20 March. If early food transfers occur on the hunting grounds, I would not have been likely to see them.

It was not clear whether the incubating female got all her food from the male or whether she also hunted. Platt (1975) states that female Gyrfalcons do not hunt from the beginning of food transferring through one week after hatching. The male at Dimmuborgir not infrequently appeared at the eyrie without prey and took over the incubation, whereupon the female left for periods of up to 4 hours. The length of her absences suggests she was hunting. However, she may have been retrieving prey the male had cached or just "relaxing." For several weeks after hatching, the female ceased any semblance of hunting, and the male then hunted for himself, her, and the young.

To give some flavor of the Gyrfalcons' behavior at this time, I quote two entries from my journal. Several explanations have been advanced to explain sexual size dimorphism in Gyrfalcons and other raptors (see Snyder and Wiley 1976). Of the several ideas Cade (1960) favors the notion that females are larger because of their need to dominate the male during the breeding cycle. One presumed reason for such dominance is to protect the young from predation by the male. However, it may be as crucial for her to be able to force the male to feed her during part of the breeding cycle. Gyrfalcons are active hunters and "jealous" of their prey. In a sense, and within limits, the female's larger size lets her "force" the male to feed her (Cade 1960). Storer's explanation (1966) puts forward the idea that the size difference allows the mates to exploit more efficiently differently sized species of prey. There is some evidence that this is the case among other raptors, especially in winter, and size differences might have some advantage for a population of Gyrfalcons that had access to differently sized species of prey. At Myvatn this advantage would likely appear during July and August. I prefer Cade's explanation because of its generality and because it seems to explain much of my data.

The first egg at Dimmuborgir was probably laid between 11 and 12 April. About 1330 on 13 April the female flew in to perch sideways on the nest ledge. The position

was somewhat unusual: her usual position was perching with her tail hanging over the edge. About 5 min later the male flew by the ledge and away, evoking a *squawk* call from the female. Nothing then happened for about 2 hours. The female remained perched on the nest ledge, facing inward, sometimes looking over her shoulder into the valley. At 1515 the male swooped up and landed on the nest ledge, to *wailing* calls, probably from the female. Both birds bowed to each other and seemed to scabble on the floor of the ledge with their beaks. While this went on, I heard a medley of *squawks*. The male then moved by the female into the nest cup, where he remained for a few moments, bowed forward. Just before leaving he half-squatted and made a motion as though muting, and then flew to a nearby ledge where he looked back over his shoulder toward the eyrie. The female remained motionless for 3 or 4 min, bowed toward the nest, then walked to its near edge and perched on its inner slope, still partly bowed over. The male left about 1530. The female remained where she was until he returned at 1700. During the hour and a half she preened for a few minutes and once gave a low *trech* almost inaudible to me, accompanied by a jerk of the head. She held the same half-bowed position.

At 1700 the male swooped up in front of the eyrie and landed above it on the butte. The female hesitated a moment, walked through the nest-cup, and flew to a nearby butte, where she perched, still tending toward the horizontal. I heard no calls. She let go with a tremendous mute, took off, circled once, and swooped up very swiftly to perch beside the male. I heard *wailing* calls, and the male plucked at a partly eaten ptarmigan carcass in his talons. The female took off again, circled, floated perhaps 6 m over the top of the butte, then settled slowly beside the male. For 3 or 4 min there was much *chittering* such as accompanied copulation. The female seemed to be pushing against the male's belly with her tail and flank. He finally moved away, and she started to pluck at the carcass. Perched upright on a rock, he let her feed for about 7 min. Normally, feedings last 20–30 min. Then he approached her from the front and after a few false tries picked up what was left of the carcass and flew away. The female remained for some minutes, picking up a few bits, and then took off, gained height, circled once very fast over the little valley, and swooped up to the nest ledge. After a few minutes she walked to the nest and climbed over it to its inner edge, where she fluffed her feathers, spread her wings, and settled down in the same half-bowed position she had been in before. She remained so for the half hour until I left at 1800.

What one might note in connection with Cade's hypothesis is the change from *wailing* calls to copulative *chittering* which preceded the male's release of his prey to the female, as well as the moderation of her movements in her second approach to him, in contrast both to her first approach and her return afterwards to the nest. She also allowed him to remove the remains from her possession. While she appeared subservient, I thought her behavior pattern implied dominance. She walked a narrow line between frightening the male away and getting him to bring her food (I do not mean to imply she was "conscious" of this).

By 28 April, incubation had been under way for about 10 days. At 1700 the male, who had been absent from the vicinity of the eyrie for at least an hour and a half, reappeared on a perch near the eyrie. The female apparently did not see him approach: the perch is not visible from the eyrie ledge. He had a full crop. After 1 hour and 45 min the male swooped up in front of the eyrie ledge to land on top of the butte. As he swooped by, I heard the *wailing* call. The female left the eggs and flew to a nearby

butte and began repeating the call. She then flew back to the butte and landed right beside the male; there was a slight scuffle in which she may have actually pushed him from his perch, upon which he flew directly to the nest ledge, walked into the nest, and began to incubate. The female settled down, feathers all fluffed out, as if to incubate, then hopped back, perched, and began to preen. She preened steadily for about 20 min, rested, then mantled and preened off and on for another 20 min, whereupon she flew. About a half hour later the male left the nest without a sound; I then heard a *wailing* call, and he swooped up as if to perch, out of my sight. I heard another *wailing* call ending in *cluckings*, and 2 or 3 min later the female flew around the eyrie butte, swooped up to the ledge, and began again to incubate.

In the light of Cade's hypothesis, I would interpret this sequence of behaviors as follows: the male made a "mistake" by landing without first showing himself to the incubating female. Recognition between the Gyrfalcons seemed to be by sight; vocalization was secondary. The male usually flew by the nest ledge or otherwise showed himself when appearing in the vicinity of the nest. He had fed, which implied, if they were sharing prey, that she was hungry. The female then acted as if she had expected him to bring food: this accounts for the "scuffle." But the male had not brought food. The female's preen and apparent "dust bath"—the sole time I saw such a performance on the top of the butte—indicated her "anxiety" or "confusion" over his not having brought prey. In this context her mantling was quite remarkable. It has been suggested to me that she was "rousing," but my journal records "mantling." Finally she left the area, perhaps to hunt, perhaps to obtain food from a cache, perhaps to exercise. Her short absence makes it unlikely, though not impossible, that she was hunting. While one can argue that the female's behavior was a result of her being "tired" of incubating and simply taking advantage of the male's presence to preen and "relax," this explanation does not adequately account for the details of her behavior, while Cade's notion does.

The female performed the main part of the incubation duty. She was not always relieved by the male while she fed. At those times the eggs remained unattended for 20–30 min. Both sexes made many of the same movements while on the eggs. They consisted of (1) an incomplete rotation, which involved a rocking from side to side of the body, a back and forth shuffling of the feet, and later a downwards bumping of the belly (these movements I assume were to accomplish a turning and regrouping of the eggs); (2) a picking up and dropping of the material in the nest cup with the beak; (3) preening; (4) snapping at flies. The time between egg turnings was variable and ranged from over an hour to a few minutes. The function of her handling of the nest cup material with her beak, if not merely a nervous release, might have been to keep the nest material, which tended to become compacted, broken up and soft and thus a better insulation against the cold. I did not observe the male handling the nest material in this way.

The mechanics of nest exchange ceremony varied greatly. The female's departure (if she was going to go) seemed to be stimulated simply by her awareness of the male's arrival in the vicinity. When she departed, the male would then either go or not go to the eggs: I could not distinguish a pattern. If he did not begin to incubate, she returned to the eggs, though sometimes with a delay of 20–30 min. Only occasionally did he initiate the exchange of incubation duties; this he did by flying to the eyrie ledge and calling gently until the female surrendered the eggs. His way of surrendering the eggs to her was also variable. Sometimes the mere sight of the returning female was enough to

make him depart. Other times he left the eggs only reluctantly and with much urging on the part of the female. I did not discover an evolution of the ceremony over time: one of the least ceremonious of the exchanges occurred on 18 May and one of the most reluctant on 19 May (both near the end of the incubation period).

From about the second week of May onward (the last two weeks of incubation), the male began to make more frequent and vocal visits to the eyrie. This behavior contrasted with his previous habit of alternating long periods in the nest area with long periods of absence. Perhaps this change was a preparation for the more frequent feeding visits after hatching. Sometimes the female left the eggs when he appeared but would immediately return to them. The male's visits were accompanied by much screaming and clucking. They did not seem to be accompanied by an increase in the frequency with which the male brought prey.

A summary of data for the incubation period at Dimmuborgir follows:

- 11–12 April, 1st eggs probably laid (13 April observation).
- 18 April, 1500, 3 eggs laid.
- 19 April, 1530, 4 eggs laid.
- 22 May, 1230, the young in at least one of the eggs squeaking. No chipping apparent.
- 23 May, 1130, 2 eggs cracked near the large end, the 3rd had a small hole on one side of the large end.
- 24 May, 1100, 2 dry young, 1 wet young, 4th egg cracked.
- 25 May, 0830, 4 dry young.

Incubation time for the fourth egg:

Maximum time—18 April, 1500, to 25 May, 0830, or 36 days, 17½ hrs.

Minimum time—19 April, 1530, to 24 May, 1100, or 34 days, 19½ hrs.

Thus the incubation period for this egg was 35–37 days. It is about a week longer than the 28–29 days reported by Brown and Amadon (1968). It is similar to the 35-day incubation period noted for captive Gyrfalcons by Cade and Weaver (1976). Platt (1976) noted 35 days for incubation of wild Gyrfalcons without specifying details. My estimate of the timing of the first egg depends on Platt's observation of 8 days for laying.

Aggressiveness toward Man. At Dimmuborgir, eyrie defense showed a definite increase up to hatching, leveled off for a few weeks, and then fell. As the time of hatching neared, the brooding female sat tighter upon my approach. Finally she let me come within about 3 m before flying and would return immediately after I left the ledge. On 23 May the pair screamed at me while I was at the nest, and on 25 May one or both stooped at me for the first time but did not come close. Thereafter their aggressiveness toward me slowly declined. On 5 June the female still stooped; on 16 June she merely flew back and forth above the eyrie screaming.

Females at Seljahjallagil and Falkaklettur were much more aggressive. The Falkaklettur female once struck me, and the Seljahjallagil female would dive repeatedly within less than 1 m of me. The aggressiveness of the female at Falkaklettur increased as incubation progressed and did not decrease after hatching. She sat much tighter than the Dimmuborgir female. Her aggressiveness seemed to be focused either on defense of the rock or (more probably) of prey, rather than on defense of the young. On 11 July, less than a week before the young left the vicinity of the eyrie, she dove repeatedly at me when I climbed the rock to collect prey remains, even though the young remained in the lava field below. She then ignored me when I tried to catch the young to weigh

them. The female at Selljahjallagil behaved similarly. On 19 July she attacked me while I was on the slope below the nest, something she had never done before. At this time, however, the slope, rather than the nest ledge, was the place to which prey was brought. At any time, the presence of more than one person made the attacks of both females less aggressive and, if I happened to arrive when they were away, the attacks upon their return seemed less vigorous.

In descending order, the aggressiveness toward me of the breeding females I was observing was: Falkaklettur, Seljahjallagil, Dimmuborgir, and Hrossaborg. The eyries with the more aggressive females were also more successful in fledging young. This observation could be interpreted as supporting the case for a relationship between female dominance and success in fledging young. One must assume that the aggressiveness of females toward a human intruder was a measure of their tendency to dominate their mates as well. It is also clear that too much female aggressiveness will create an impossible breeding situation: what is required is the proper aggressive balance for a pair. Although the females that were the most aggressive toward me were also the most successful in raising young, the second most aggressive female raised what appeared to be the most healthy and vigorous young. The male of that pair was also considerably more aggressive toward me than the males at other eyries. The Falkaklettur male seemed to visit the nest very infrequently and cautiously, which may have been a sign of his fear of the female. The whole issue of success in fledging young becomes confusing because of the different locations of the nests, the implied differences in prey available, and the differences in the hunting abilities of males. These factors may also be related to aggressiveness, but not solely to it.

Nestling Period. Most of my information concerning the nestling period comes from the Dimmuborgir eyrie.

After hatching, the male did all the hunting. Brooding by the male was rare. Twice I saw him begin to brood the young while the female left to carry off prey remains. Jenkins (1974) reports brooding of the young by the male while the female fed.

I saw only the female feed the young. She always took some of the prey for herself, and on at least one occasion (27 May), she fed herself from a carcass before bringing it to the chicks. Usually she fed herself and the young concurrently, concentrating first on the young, then for a while on herself, then on the young again. Such feedings usually took 20 to 30 min. Wayre and Jolly (1958) report feeding times at a Myvatn eyrie of about 16 min and state that feeding by the male was not uncommon. After feeding, the remains of the prey were sometimes removed, usually in the feet. Twice the female left carrying such remains in her beak. Because of this removal I could not calculate the total amount fed. I could not discern a regular daily pattern in feeding. Some days had many and other days few feedings.

The ceremony surrounding the exchange of prey between male and female had become quite regular by the time of hatching. In the first weeks after hatching, while the female was remaining near the young or in the immediate vicinity of the eyrie, prey exchange occurred near the eyrie, as it had during incubation. A relative innovation was the commencement of *wailing* calls by the female after receiving prey, or after arrival of the male without prey. Sometimes she stopped such calls by herself and sometimes only after the departure of the male, who during incubation often stayed in the area for an hour or so after bringing prey. In the most remarkable instance (in this case he had brought in prey) she called continuously for 16 min until he left the area. Jenkins (1974)

reports the caching of uneaten remains about the nesting cliff. This I did not observe.

During the first week after hatching, the female spent most of her time brooding, leaving the nest for only short periods. By the second week, the single remaining young had grown sufficiently to move about the nest and disturb the brooding female. She still spent most of her time brooding, leaving only for short periods. During the second week I heard the young calling during feeding periods. Begging consisted of shaking the raised head stiffly back and forth and calling.

By the middle of the third week the chick at Dimmuborgir was too big to brood comfortably, but the female still spent most of her time standing over or near it. Brooding at Falkaklettur stopped during the third week. This eyrie had three young, however, and brooding probably became physically impossible as well as unnecessary earlier. Wayre and Jolly (1958) report that brooding was over by the fourth week, but that the female remained almost constantly in the vicinity of the eyrie. During the third week at Dimmuborgir the young began to take a more active part in the feeding process and often, when the female held a bit of food before it, would move to take the food from her beak.

By the middle of the fourth week the young at Falkaklettur were flapping their wings. Wayre and Jolly (1958) report the same observation. At Dimmuborgir, from my observation post, quills became visible through the down during the fourth week, and the chick also began preening and flapping its wings. Cade (1960) assumed young gyrs are 3 weeks old when quills showed. The young now moved vigorously about the nest and called. The female was still spending most of her time in the nest near the young but would leave the nest for periods of more than an hour.

During the fifth week the Dimmuborgir female abandoned her position in the nest for one on the eyrie ledge, and by the end of the fifth week she abandoned the ledge but still remained in the area. Her *wailing calls* were becoming hoarser, more like those of early March. On 27 June (nestling about 33 days old), she left the eyrie area for an hour and a half.

During the fifth week the chick bent toward the prey as the female fed herself. Every now and then it managed to steal a few bits from the carcass or from her beak. On 27 June it moved to the edge of the ledge to mope. The mope shot clear of the ledge. Jenkins (1974) connects this practice and the removal of prey remains with the need for nest sanitation—to minimize infection of young by parasites or disease. But removal of prey remains seems to be practiced irregularly. Bengtson (1971) reports “heaps of remains” under some nests. I saw a similar condition at Gyduhnjuksgil, where rotting remains were scattered on ledges all over the cliff. It may be that as long as the remains are off the nest shelf the dangers of parasite buildup are minimized; such removal tends to occur naturally with older young, who knock them off. Furthermore, adults presumably suffer some risk to themselves in trying to remove remains from under the feet of well-grown young. The removal of remains by the adults might then be restricted to the early weeks of the nestling period. The accumulations found under nests would occur in later weeks. Removal of remains from the eyrie area by the gyrs early in the nestling period would tend to bias late-season prey collections against prey taken preferentially early in the season.

During the sixth week the Dimmuborgir young began to feed itself, and the female apparently began to hunt again.

If the Dimmuborgir female began to hunt between 27 June and 2 July, she began

comparatively early. The gyrs at Falkaklettur and Seljahjallagil bred slightly earlier. At Seljahjallagil, the female could have been hunting on both 13 and 19 July and almost certainly was by the 25th. I do not think the female at Falkaklettur was hunting on 11 July, though I assume she had begun by 13 July, when the eyrie was deserted. Thus, allowing for the difference in the breeding cycle, the females in the last two eyries started hunting between 3 and 4 weeks. Cade (1960) states that in the latter days of the nestling period both the male and female hunt; Wayre and Jolly (1958) found a Myvatn female hunting during the fourth week of the nestling period.

Fledgling Period. Jenkins (1974) reports 45–47 days for fledging. On 9 July the 8-week-old young at Falkaklettur were flying. On 12 July I found the 7-week-old young at Dimmuborgir dead on the slope below the eyrie. It had been alive on 9 July, with the female present. It was fully fledged and weighed 660 gm. The young at Seljahjallagil, which were less than a week older, all weighed more than 1000 g on 13 July.

The Falkaklettur eyrie was empty when I visited it on 13 July but showed signs of some further use (juvenile down, prey remains) when I visited it again on 7 August. The adults brought food to the young at Seljahjallagil at least until 3 August (their 11th week). I did not visit this eyrie again until 19 August (the 13th week), when it was deserted except for a pair of scavenging ravens. Bringing the prey to a central feeding place (first the eyrie ledge, then the slope below) ceased between 19 and 21 July. From 21 July on, remains were scattered all over the canyon. Cade (1960) mentions a brood of young gyrs that were flying on 10 July and still near the eyrie the second week of August. Bengtson (1971) states that Gyrfalcon eyries at Myvatn are “abandoned” the last week in June or first week in July.

I first saw young Gyrfalcons near the lake on 28 July (the 10th or 11th week for juveniles) and after that found signs of them along the east shore. I did not see adults in their company, but I had them under observation too briefly and too infrequently to know if they were still being fed by adults. Eyries at Gaesadalur and Gyduhnjuksgil, which had both raised young, were deserted when I found them on 17 and 12 August, respectively (the 12th or 13th week for the other broods).

Generally, then, it seems that within 2 or 3 weeks of learning to fly the young start to follow their parents to the hunting grounds. At this time these grounds are the shores of the lake, which from mid-July to mid-August are home for thousands of young and vulnerable ducks, shorebirds, and gulls. The eyrie areas are now either abandoned or used only sporadically. Platt (1976) reports observations by Wiseley and Kosler of apparent “family groups” of juvenile Gyrfalcons still together on the “hunting grounds” in September. Whether the young were still being fed by the adults was not clear.

Adults appeared to cease feeding young toward the end of August. I spent 24–27 August on Hrisey, an island off northern Iceland with a large breeding population of Rock Ptarmigan. This would be the 14th week for the Myvatn juveniles. At this time, two juvenile Gyrfalcons were apparently successfully feeding themselves on juvenile ptarmigan that they caught on the ground. The presence of the young gyrs on this island in the middle of the fjord, 4 km from the mainland and probably at least twice that from their eyrie, strongly suggests that the young followed the adults there.

The productivity of 1967 is shown in table 1.

Table 1. Productivity of Gyrfalcon Eyries near Myvatn in 1967.

Eyrie	Eggs	Eggs hatched	One week	4-5 wks	Fledged & flying
Dimmuborgir	4	4	4	1	0
Falkaklettur	4	?	?	3	3
Seljadalur	0				
Seljahjallagil	?	?	?	4	4
Dalfjall	0				
Vindbelgjarfjall	0				
Gaesadalur	?	?	?	?	?°
Gyduhnjuksgil	?	?	?	?	?°
Hrossaborg	?	?	?	3	0 ¹

*Unknown number of young raised to flying age in each case.

¹Four young were present on 19 June, three on 24 June (when the wing quills were poking through). All were dead in the nest on 26 June. The cause of death was probably starvation. Between 19 and 24 June a photographer set up a blind about 50 m from the nest; I dismantled the blind on 24 June. By then one young was apparently dying, and the other two were quite lethargic. Neither adult appeared during the hour we spent there. The three dead young are presently in the collection of the Museum of Natural History, Reykjavik.

Agonistic Behavior

Interspecific. Three predatory birds—the Common Raven, the Gyrfalcon, and the Merlin—are regular summer residents of the Lake Myvatn basin. The raven and Gyrfalcon remain in the region for much of the year; the Merlin is migratory. Except for a small over-wintering population of ducks—primarily Barrow's Goldeneye (*Bucephala islandica*), Goosanders (*Mergus merganser*), and Mallards (*Anas platyrhynchos*)—the only prey available to Gyrfalcons during the winter and early spring is ptarmigan. Ravens are both predators and scavengers. They probably scavenge prey remains left by the gyrs, but the importance of such remains in their diet is unknown. Judging from signs about the remains, the ravens, at least in winter, face considerable competition for them from Arctic foxes.

The three predators often nest near each other. The situation in 1967 is detailed in the eyrie description under *The Eyries*. I did not make an exhaustive search for raven or Merlin nests, but nesting associations seemed to be the rule rather than the exception. The only nests of either Merlins or ravens of which I was aware, other than those near Gyrfalcon eyries, were two suspected eyries of Merlins. The frequent use of raven nests by gyrs might help explain the gyr-raven association, but the Merlin-gyr association remains something of a mystery. There does not seem to be a lack of suitable geological structures for nest sites for any of these species in the Myvatn basin. However, various writers have reported finding Gyrfalcons nesting near other raptors. Hagen (1952) reports eyries of the Gyrfalcon and the Rough-legged Hawk (*Buteo lagopus*) within 60 m of each other. White and Cade (1971) report nests of the Gyrfalcon and Peregrine within 40 yds and those of the Gyrfalcon and raven within 20 yds. In no case did I find nests closer than 200 m. White and Cade (1971) suggest ravens use Gyrfalcons' cliffs in order to scavenge the gyrs' prey remains. I saw no scavenging near the nest cliff itself as long as the Gyrfalcons were in residence.

I saw two aggressive encounters between Merlins and gyrs. On 17 May in Dimmuborgir, the male gyr returned about a minute after leaving the eyrie with a Merlin stooping at him but not touching him. After two or three stoops the Merlin departed. It did not follow the gyr into the immediate vicinity of its eyrie. The gyr ignored the attack and soared over the eyrie upon his return.

The other incident occurred at Vindbelgjarfjall, where the Merlins were nesting and the gyrs not. In this case, the male Merlin attacked one of the gyrs that flew in right over its nest. The Merlin chased the gyr into the gyrs' usual perching area, then dislodged either it or another from a perch, and finally dove again and again at one while the other circled nearby. Eventually the Merlin departed, and the gyrs returned to the cliff. One of the gyrs was screaming at the beginning of the attack, but neither attempted to attack the Merlin.

The one case of clearcut competition for nest sites occurred at Seljadalur. During March and April a pair of ravens and a pair of gyrs shared the canyon in apparent peace. The gyrs used the valley (mostly, however, the west cliffs which had not been used for nesting by either species) for roosting and perching. The ravens started building a nest on the east cliffs (the traditional nesting cliffs) about 1 April. As far as I could tell, the gyrs did not pick a nest site, though I found some evidence of scraping on a ledge on the west cliffs on 27 April. A nest here would have been right across the narrow canyon from and in full view of the raven nest. A nest in the former gyr site (old raven nest) would have been level with, in sight of, and perhaps 30 m from the new raven nest. The ravens began to brood about 27 April. On 30 April, alerted by excited croakings from the ravens, I saw a gyr (probably a male) make a feint at a raven perched on a ledge of the east cliffs. It did not actually strike the raven, both birds flew up, the raven got above the gyr and lunged down, and both birds fell almost to the valley floor, turning round and round and apparently grappling. Then the gyr flew straight away screaming with the raven in pursuit. A few minutes later the raven returned to the canyon.

On 8 May I arrived at 0500 at Seljadalur. As on 11 April, the ravens were then active. The gyrs became active about 0800. The gyrs were roosting in the canyon, and a ledge of the east cliff above and upvalley of the raven nest showed much new use by gyrs. The ravens did not follow me to this area of the cliff. No interaction occurred this morning though both species were present. I heard what sounded like a quarrel on 13 May, perhaps stimulated by a low-flying airplane (a rare occurrence which usually brought the gyrs into the valley). The gyrs continued to use that ledge at least into July.

Interspecific competition may have prevented the Gyrfalcons in Seljadalur from nesting, but I doubt it. April 27 is at least a week later than any of the other Gyrfalcons in the area began laying. Moreover, two other pairs of gyrs near the lake also failed to lay. The Seljadalur gyrs were successful in establishing themselves on the east cliffs and seemed content there. Although competition with the ravens provided yet another stress, I suspect the primary stress causing nonbreeding at Myvatn in 1967 was a relative lack of prey.

I saw one agonistic encounter between ravens and gyrs that was apparently over hunting grounds. On 19 March I was coming across the lake on the ice toward a shrubby hill where I frequently found either gyrs or ravens, when I saw a raven and a gyr above the hill, each of them calling and circling. At first, the raven, who had the height advantage, dived at the gyr, then it ceased diving but kept its advantage. The gyr eventually broke off and flew down to perch on a rock, after which the raven descended, but did not land. It was joined in the air by another raven. The ravens flew off together, and the gyr remained perched.

During the summer, gyrs that hunted from perches along the lakeshore were struck at by passing Arctic Terns (*Sterna paradisae*). It seemed an almost casual display of antagonism. The Gyrfalcons would flinch but not fly, and the terns never seemed to gang up to drive it away.

Intraspecific. I observed no intraspecific quarrels over perching posts or hunting grounds. In fact, there was some indication that, at least in March and April, hunting grounds were shared by gyrs of different pairs. The only space I saw defended from other gyrs was that immediately about the eyrie.

On 16 June the male returned to the Dimmuborgir eyrie from a 2-hour absence in an unusual fashion—slowly circling, both gliding and flapping, toward the eyrie butte. Both performing such a display upon his return and the form of the flight movements themselves were unusual. He was not high, passed over the eyrie and beyond, then returned. The female saw him but did not respond. Suddenly she left the eyrie, and I saw a third gyr flying overhead on a path that would take it right over the eyrie (toward Seljahjallagil). Both gyrs were on the interloper immediately. First the female grappled at it from below, and then the male dropped on it from less than a meter, so that it had to flip over and present its talons upwards. It was attacked once more, then merely closely followed, until they were 200–300 m south of the eyrie, when the pair broke off and returned, gliding close together, then soared separately over the eyrie for about 10 min, keeping within a radius of perhaps 250 m. At this time (2 weeks after hatching) the pair was at the peak of their aggressiveness toward me. Earlier in the season the incubating female had shown some reaction (once even leaving the nest) to Greylag Geese (*Anser anser*) that passed directly overhead.

Finally, at Vindbelgjarfjall on 26 April I watched the adults chase away (perhaps, “escort away”) two gyrs in juvenile plumage. I had been watching the cliff for 2 hours when the adults appeared. One landed in view, and the second disappeared into a cut in the cliffs and began to scream excitedly. At this point a juvenile flew from behind me, heading toward the cliff, and the adult reappeared from the cut, followed by another juvenile. The three gyrs on the wing flew screaming along the face, the other adult then joined them, and all four flew out of sight around the mountain. An adult soon returned, circled, and disappeared into the cut. The other adult appeared and perched on the open face. In about 2 min the juveniles returned from the direction in which they had gone, one flying straight for that invisible ledge in the cut. Both adults then gave chase, sometimes dropping down toward a juvenile from just above it but for the most part just staying near the young birds. Once a young bird flipped on its back as though to grapple with an adult. An adult circled back and began to land, when a juvenile flew right over its head, not making any move down toward it. The adult flinched, I heard screams, and the two flew away along the cliff. I heard more screams after about a minute and saw a gyr circling, but then all was quiet. A search of the part of the cut that had seemed so intriguing revealed the fresh carcass of a ptarmigan on an inaccessible ledge.

This occasion was my only certain sighting of juveniles from the previous year at Myvatn.

Sharing of Hunting Grounds

Several times in March and early April, up until cock ptarmigan began setting up territories, I saw what were apparently Gyrfalcons from different eyries hunting the birch scrub northwest of Dimmuborgir, at distances of from 2 to 5 km from the Dimmuborgir eyrie. Cade’s (1960) schematic of the breeding territories of Peregrines along the Yukon River implies that the outer parts of the territories may be shared in this species. Whether Gyrfalcons usually share, or do not defend, their home ranges, except for a limited area about the eyrie, is unclear. The only territory I saw defended from other gyrs was that immediately about the eyrie. I did see a Gyrfalcon drive a pair of ravens

from what was a favorite hunting area for both species. The spot was 4 km from the Dimmuborgir eyrie (the closest).

In late winter and early spring ptarmigan are virtually the only food available to the Myvatn Gyrfalcons. Since at this time the ptarmigan feed heavily on birch catkins, birch shrubland is the favored hunting ground for the gyrs. Such shrubland is limited in extent, and the ptarmigan population of a given piece of it seems to fluctuate daily. Thus a certain amount of pressure exists for sharing hunting areas. When about the middle of April the cock ptarmigan set up territories and spread out over larger areas, this pressure would appear to be reduced. Such pressure might rise again in late June, over areas favored for the taking of ducks, gulls, or shorebirds.

Nest-Site Selection

Cade (1960) states that 18 of the 21 Gyrfalcons eyries he found along the Colville River were overhung. He thought that the extensive use of old raven nests by gyrs in part explains the overhangs. Ravens, like gyrs, nest before melt-off and choose an overhung site for its protection from the snow.

To test this hypothesis I noted the snow cover on several overhung and non-overhung former eyrie sites during March and April. The overhangs did not seem to make much difference to snow cover. In fact, the high winds frequent to the area sometimes blew the exposed ledges clear while drifting over the overhung sites. My chief non-overhung site, an old raven nest in Seljadalur, did not seem to accumulate more than a few inches of snow at any time.

Unfortunately these observations cannot be taken to mean that snow cover is not a factor in nest-site selection by ravens and gyrs, nor that overhangs may not, in many situations, prevent snow and ice from building up on a potential nest site. However, especially among ravens, the choice of an overhung site may have to do with something other than snow cover—concealment of the nest, for instance.

Hunting

On 4 March I watched Gyrfalcons attempt two kills. The first resembled the "tail chase" described by Cade (1960), White and Weeden (1966), and Bengtson (1971). It was snowing, and I had picked a spot to sit where I had seen ptarmigan the day before. After I had been there about 15 min, a ptarmigan flushed, about 40 m away. Ten min later a ptarmigan flew over my head with a Gyrfalcon about a meter and a half behind it and gaining altitude. The ptarmigan dived into the scrub, whereupon the falcon turned abruptly and plunged down into the scrub also. They were then about 60 m away. Five min later the gyr reappeared from the same spot without prey. Later, I saw a gyr flying over the scrub turn abruptly and dive down, seemingly to the ground. Twenty sec later the gyr reappeared and flew away, whether with or without prey I could not tell.

These incidents differed from what I saw when the ptarmigan were displaying in that there is some suggestion that the Gyrfalcons sighted its prey while flying. In March I occasionally saw gyrs flying low over the scrub. The ptarmigan along their flight path either froze or flushed, in the latter case exposing themselves to pursuit. However, I never saw a gyr strike in this situation. Similarly, ducks often flew rather than swam away if they were too close to perched falcons. Flying is faster, but I would think swimming is safer. However I never saw a Gyrfalcon strike at flying ducks in this situation either.

The most common method of hunting at Myvatn seemed to be the "sneak attack" from a perch. The gyrfalcon watched from some advantageous (not necessarily very spectacular) lookout, and then flew, dropping down almost to the ground and moving with startling rapidity just over the ground or the scrub toward an unsuspecting, nonflying prey. I saw this method used once in March against ptarmigan and again in August against shorebirds, but it was most apparent during the display period of the cock ptarmigan. A search of a busy moor often revealed a Gyrfalcon, perched motionless, watching the activity of the noisy cocks around it. By June it seemed as if every other ptarmigan display post had a few feathers or a wing from a previous occupant. Bengtson (1971) reports similar observations and states that the most common hunting technique was the snatching from the ground, or more rarely water, of an unsuspecting prey.

Both White and Weeden (1966) and Cade (1960) mention a high flight by Gyrfalcons, which they connect with hunting behavior. Bengtson (1971) saw soaring frequently. I observed soaring in several different situations. Two had to do with display. Soaring preceded mutual gliding at Seljadalur and followed an attack on an intruding gyrfalcon at Dimmuborgir. On 13 June the female at Falkaklettur soared until almost out of eyesight (about 350 m up) and then traced a great circle about the eyrie in what was apparently either a signal to or a search for the male, which had not come with prey for the 8 hours I had been watching. She returned in about half an hour, overheated, without the male and without prey. The Seljahjallagil pair often soared at 200–300 m when leaving the lake for the lakeshore and vice versa, when returning with prey. It was undoubtedly an easier way than direct flight to cross the 7–8 km of sandy waste that intervened. White and Cade (1971) suggest that Gyrfalcons may go up to 10 miles from the nest to obtain prey. The restricted location of available ducks, gulls, and shorebirds in midsummer at Myvatn makes commutes of somewhat lesser distances necessary for several of the Myvatn eyries. I saw adults at Seljahjallagil returning with prey from the direction of the lake and leaving the lakeshore with prey in the direction of the eyrie.

Finally, the male at Dimmuborgir sometimes soared, but not so high, and then went into a long glide when leaving the area. In short, I did not see soaring, or soaring and gliding used by Gyrfalcons for hunting, but only for travelling and display.

Treatment of Prey

Finnur Gudmundsson (pers. comm.) suggested that one difference between the treatment of prey by Gyrfalcons and ravens is that, while both species pluck their prey, only Gyrfalcons pluck the primaries. Hagen (1952) reported that in 31 Gyrfalcon kills all had had some primaries plucked. Of the wings of the approximately 250 Gyrfalcon kills that I examined, only one had not had at least one primary plucked. The number of primaries plucked varied from 1 or 2 to virtually all. Most of the carcasses I inspected were from eyries with young, and casual observation indicates that such remains are handled much more extensively than those killed and eaten by adults elsewhere. But carcasses of Gyrfalcon kills from the prehatching period and from the early flying stage (when the amount of handling seems to decrease) also had plucked primaries.

I noted three other characteristics of Gyrfalcon kills. In smaller-boned prey, such as ptarmigan, the head is almost always eaten. It is apparently bitten off from the back. The mandibles can often be found, sometimes with enough of the frontal skull attached to determine the sex of the bird. Hagen (1952) reports not finding heads among the remains, the implication being that they are discarded or eaten. Secondly, a length of intestine and sometimes the gizzard are removed and discarded. I found such lengths near

kills "in the field" and at eyries after the young had fledged. Hagen (1952) reports that the "intestines (gizzards)" tend to be eaten, but he may be simply saying that they were missing from the kills. In April after snow thaw I found many mats of discarded intestines along the base of the Dalfjall ridge, with both bird mutes and fox scats next to them. The mutes could have been from either Gyrfalcons or ravens. The intestines appeared to be all that remained of Gyrfalcon kills that had been scavenged by ravens and foxes. The scavengers apparently were not interested in the intestines either. Finally, the Gyrfalcon does a neat job. The breast is cleanly stripped of flesh, as may also be the legs and wings. With smaller prey, the keel may have large bites taken out of it or be eaten completely down. The raven's work tends to be cruder in appearance.

Prey of the Gyrfalcon

In compiling prey remains (tables 2, 3, 4), I took Cade's (1960) approach to numerical estimation. I matched right and left wings by sex and species and then with sterna or

Table 2. Prey Remains Collected from the Falkaklettur Eyrie in 1967.

	6/2°	6/13°	7/3	7/9	7/11°	7/17 ^f
Ptarmigan (<i>Lagopus mutus</i>)	34 ^a	6	45 ^b	15 ^c	6 ^d	3-4
Mallard (<i>Anas platyrhynchos</i>)						
Gadwall (<i>Anas strepera</i>)			1			
Wigeon (<i>Anas penelope</i>)			3	1		1
Pintail (<i>Anas acuta</i>)						
<i>Anas</i> spp.				2		
Tufted Duck (<i>Aythya fuligula</i>)			2			1
Scaup (<i>Aythya marila</i>)			1	1		
<i>Aythya</i> spp.				1		
Old Squaw (<i>Clangula hyemalis</i>)						
Barrow's Goldeneye (<i>Bucephala islandica</i>)						1
Red-breasted Merganser (<i>Mergus serrator</i>)						
Common Scoter (<i>Melanitta nigra</i>)						
Duck spp.			2	4	1	
Total ducks (%)	0 (0)	0 (0)	9 (16)	9 (35)	1 (10)	3 (38)
Black-headed Gull (<i>Larus ridibundus</i>)				1 ^h	3 ^e	1 ^g
Golden Plover (<i>Charadrius apricarius</i>)				1 ^h		
Whimbrel (<i>Numenius phaeopus</i>)			1			
Redwing (<i>Turdus iliacus</i>)			1 ^h			
Unknown			1			
Total other than ptarmigan (%)	0 (0)	0 (0)	12 (21)	11 (42)	4 (40)	4 (50)

Estimated date of hatching May 20-25.

*Remains in the eyrie and immediately about it not collected, or lost.

^a12 old, 22 new.

^b33 old, 4 new, 8 uncertain.

^c10 old, 5 new.

^d6 old.

^e2 juvenile, 1 of unknown age.

^fEyrie deserted at least 2 days before. All the prey remains were fresh.

^gAge unknown.

^hJuvenile.

other body parts present. Backbones, while used as a rough check on the total numbers of prey collected, were, because of the difficulties in identifying them, not associated with the rest of a skeleton. It was often possible to check such skeletal reconstructions by trying the fit of bones into corresponding sockets.

Ducks were difficult to identify. A. Gardarsson assisted me in their identification. Primaries had usually been plucked entirely except for two or three; and we had to work with what few feathers remained and the general size and shape of the skeleton. Unfortunately, the soft sternal edges and keel, whose outlines are useful in separating the duck species, were habitually bitten away. Feathers commonly left included one or more of the following: upper and lower leading wing edges; scattered primaries and secondaries; scapulars; coverts; or a tuft from the side of the breast.

The tables do not provide a reliable chronological estimate of prey brought to the eyries because of the removal of remains from the nest vicinity by adults. Such removal was rather irregular. At Dimmuborgir it became more frequent after hatching. Some

Table 3. Prey Remains Collected from the Dimmuborgir Eyrie in 1967.

	6/3	6/5	6/16	6/27	7/3	7/12 ^a
Ptarmigan (<i>Lagopus mutus</i>)	19	3	6	4	5	4
Mallard (<i>Anas platyrhynchos</i>)						
Gadwall (<i>Anas strepera</i>)						
Wigeon (<i>Anas penelope</i>)			2	9	3	3
Pintail (<i>Anas acuta</i>)						
<i>Anas</i> spp.				1		
Tufted Duck (<i>Aythya fuligula</i>)						2
Scaup (<i>Aythya marila</i>)						
<i>Aythya</i> spp.					1	
Old Squaw (<i>Clangula hyemalis</i>)				1		
Barrow's Goldeneye (<i>Bucephala islandica</i>)						
Red-breasted Merganser (<i>Mergus serrator</i>)						
Common Scoter (<i>Melanitta nigra</i>)						
Duck spp.						3 ^b
Total ducks (%)	0 (0)	0 (0)	2 (25)	11 (73)	4 (44)	8 (67)
Black-headed Gull (<i>Larus ridibundus</i>)						
Golden Plover (<i>Charadrius apricarius</i>)						
Whimbrel (<i>Numenius phaeopus</i>)						
Redwing (<i>Turdus iliacus</i>)						
Unknown	1	1 ^c				
Total other than ptarmigan (%)	1 (5)	1 (5)	2 (25)	11 (73)	4 (44)	8 (67)

Date of hatching, May 25.

^aThe nest had been abandoned at least one day before.

^bOne of the ducks was a duckling.

^cA small, blue, maggot-infested duck foot. The unknown on 3 June consisted of a matched radius and ulna. The foot appears to antedate this collection, and the two remains may be from the same bird.

remains were dropped within 100 m of the eyrie, others carried further off (see Weir 1967). The more distant remains were probably quickly scavenged by ravens or Arctic foxes.

Collection problems at the Falkaklettur and Seljahjallagil eyries included the appearance of old ptarmigan remains along with the new ones in my weekly or fortnightly collections—apparently because I never found all the remains at any given time. The aggressiveness of the females at these eyries made collection difficult. Both sites had been used in the recent past, and the slopes beneath were speckled with bits of remains. Remains of smaller prey get broken badly by the young if they remain in the eyrie over any period of time. They dry out rapidly and blow about: some undoubtedly get lost. Old remains may get dug out of the mud of the eyrie shelf. Since I found it difficult to be absolutely sure about what was old and what new, I composed the tables according to what was picked up with the “old” and “new” designations in footnotes.

With these qualifications, the data in the tables suggest that there was a shift in the prey taken, from ptarmigan to other species, that occurred from the second week of June onward. Prior to 16 June the only remains I found at Dimmuborgir, with two exceptions, were of ptarmigan. On 16 June I found remains of two Widgeon (*Anas penelope*) along with six ptarmigan, and on 27 June, nine Widgeon, two unidentified ducks, and four ptarmigan. At Falkaklettur I found the first remains other than ptarmigan on 3 July. Thus at Dimmuborgir the shift began between 5 and 16 June and at Falkaklettur between 13 June and 3 July. The Falkaklettur eyrie was situated in an area where prey other than ptarmigan was either scarce or a considerable distance away.

The shift in prey can probably be correlated with changes in the behavior of the cock ptarmigan. When I arrived at Myvatn in early March, the chief prey of the Gyrfalcons appeared to be ptarmigan. At the same time, ducks were present in some numbers. A count on 3 March along 4 km of the lake (including most of the lake that remains open during winter) gave 170 Barrow's Goldeneye (117 males, 53 females), about 100 Goosanders (*Mergus merganser*) (sexes equally divided), about 45 Mallards (*Anas platyrhynchos*) (30% females), along with 37 Whooper Swans (*Cygnus cygnus*). The ducks did not appear to be taken in any numbers. Migratory waterfowl begin arriving in mid-April. By May they are present in force.

About the middle of April ptarmigan cocks begin to set up territories. For the next 2 months predation seemed to fall heavily on them. The cocks keep their white plumage and preoccupation with territorial defense into early June. Thus they remain vulnerable to Gyrfalcons predation through the beginning of that month. Signs of Gyrfalcons predation on ptarmigan cocks in the form of remains on (reoccupied or unoccupied) display posts are common during the display period.

In June, when the ptarmigan egg clutches are complete, the cocks acquire summer plumage and become much less territorial and more skulking in behavior. There is still some erratic display, especially at twilight, and since Gyrfalcons hunt at night in summer, the cocks remain still somewhat vulnerable. In the Myvatn area this midnight display activity continued into July.

For the Gyrfalcons, the change in the behavior of the cocks comes at a pivotal time—a week or two after the young have hatched and need a large and regular supply of food. The male, which ordinarily does all the hunting during the first part of the nesting stage, must now hunt for the equivalent of three adults or more. Thus he has a powerful stimulus to break whatever “fix” he has on ptarmigan and to turn to other species.

Table 4. Prey Remains Collected from the Seljahjallagil Eyrie in 1967.

	6/30	7/7	7/13	7/19
Ptarmigan (<i>Lagopus mutus</i>)	11	4	17 ^a	17 ^b
Mallard (<i>Anas platyrhynchos</i>)		1	3	
Gadwall (<i>Anas strepera</i>)				1
Wigeon (<i>Anas penelope</i>)	3	2	4	2
Pintail (<i>Anas acuta</i>)	1			
<i>Anas</i> spp.			6	1
Tufted Duck (<i>Aythya fuligula</i>)	7	1		3
Scaup (<i>Aythya marila</i>)	4	3	1	2
<i>Aythya</i> spp.	5		2	2
Old Squaw (<i>Clangula hyemalis</i>)	2	1	1	
Barrow's Goldeneye (<i>Bucephala islandica</i>)		2		
Red-breasted Merganser (<i>Mergus serrator</i>)				1
Common Scoter (<i>Melanitta nigra</i>)		1		
Duck spp.	7	11	7	1 ^c
Total ducks (%)	29 (73)	22 (81)	24 (53)	13 (34)
Black-headed Gull (<i>Larus ridibundus</i>)		1 (juv)	4 ^c	8 ^d
Golden Plover (<i>Charadrius apricarius</i>)				
Whimbrel (<i>Numenius phaeopus</i>)				
Redwing (<i>Turdus iliacus</i>)				
Unknown				
Total other than ptarmigan (%)	29 (73)	23 (85)	28 (62)	21 (55)

Estimated date of hatching May 20-25.

- ^a 10 old, 7 new.
^b 15 old, 2 new.
^c 1 juvenile, 3 unknown age.
^d Age unknown.
^e Duckling of diving duck.

The completeness of the shift probably depends on the availability of these species to individual Gyrfalcons. Since habit enters in, and chance falcon-ptarmigan encounters occur, one would not expect a complete shift in most cases. As mentioned above, Gudmundsson and Gardarsson found that predation by Gyrfalcons on the nesting ptarmigan of Hrisey virtually ceases in early June. Hrisey is about 4 km from the nearest point on the mainland and likely at least twice that from the eyrie from which they surmised the Gyrfalcons are coming. In such a situation, where Gyrfalcons come from a considerable distance to hunt an island almost exclusively for ptarmigan, and where "reservoir species" exist elsewhere, the shift might appear much more complete. An investigator collecting remains from the eyrie of those same Gyrfalcons might continue finding ptarmigan that were picked up closer to the eyrie.

A corollary of the shift in prey seems to be that the presence of one or more “reservoir species” is helpful for the successful raising of young by Gyrfalcons whose primary prey is ptarmigan, especially in years of marginal ptarmigan populations, where perhaps ptarmigan are abundant enough to induce the Gyrfalcons to breed, but not abundant enough to ensure survival of the young. Cade (1960) and White and Cade (1971) describe situations somewhat like this along the Colville River in Alaska. The Colville Gyrfalcons prey almost exclusively on ptarmigan, and their breeding success, or whether they will breed at all, fluctuates with the ptarmigan population. In 1959 Cade (1960) observed a shift to rodents and rodent-eating birds about the middle of June. He explained the shift by the concurrent departure of a high late-winter ptarmigan population, which had induced a record number of Gyrfalcons to breed, and the snow melt-off that exposed a peak rodent population. The rodent population attracted many non-breeding, rodent-eating birds that were highly vulnerable to Gyrfalcon predation. Cade’s explanation is rather speculative, and it is difficult to assess whether the shift in prey was motivated by a special situation or whether pressure exists for it annually.

Hagen (1952) describes an apparently marginal breeding situation for ptarmigan-dependent gyrs in the Norwegian mountains, in which successful breeding in a certain valley coincided with peak rodent years. Rodents were not important in the diet of the Norwegian Gyrfalcons. Hagen speculates that the coincidence has three causes: (1) Less pressure from other predators makes Willow Ptarmigan (*Lagopus lagopus*) live more openly in peak rodent years (an observed fact); (2) competition between carnivores is reduced in high microtine-rodent years; and (3) the two *Lagopus* species that form the bulk of the Gyrfalcons’ prey tend to fluctuate with the microtine-rodent cycles and are more abundant in years of high microtine population. Thus, in a situation where a satisfactory reservoir species for the gyrs apparently does not exist, other factors tend to create the same effect in certain years.

Bengtson (1971) reports data concerning a prey shift in Myvatn Gyrfalcons, in the form of prey being transported by flying Gyrfalcons. For ducks being transported in the months May through August, the numbers are 15, 10, 20, 20; for Rock Ptarmigan in the same months, the numbers are 9, 8, 3, 1. Thus Bengtson observed an increase in ducks being carried in July and August, and a decrease in Rock Ptarmigan during those months. Bengtson’s studies focused on the waterfowl population, and there is no way of knowing how random his sample was. It may be biased toward ducks. He certainly records relatively more ducks being taken in May and June than I observed. However, this situation may vary from eyrie to eyrie and year to year. For instance, the Vindbelgjarfjall eyrie, unproductive in 1967, is located amidst some of the best waterfowl habitat at Myvatn. Parts of their hunting grounds for ptarmigan are also good waterfowl habitat. It would be surprising if this pair did not take waterfowl in substantial numbers early in the season.

My data suggest the tendency toward specialization at the three eyries on Widgeon, Tufted Duck (*Aythya fuligula*), and Scaup (*Aythya marila*). Much has been written about the Gyrfalcon’s tendency to develop a “fix” on prey, and these data perhaps support the notion. There is some question in my mind about whether such “fixes” are the result of prey behavior or prey presence. The three ducks in question are also the three most common species at Myvatn, according to Bengtson (1971). Even more to the point, as I have tried to show, a Gyrfalcon hunting ptarmigan in May faces quite a different situation from one hunting them in March.

Distribution of Nests

If one ignores the eyrie at Seljadalur, all the eyries to the east of the lake were spaced between 9 and 11 km apart. This distribution suggested that perhaps the gyrs at Seljadalur and Dalfjall failed to breed because their potential nests were "psychologically" too close together. If the gyrs at Holkotsgil were not the same as those at Vindbelgjarfjall, this hypothesis would also explain the nonbreeding at Vindbelgjarfjall. However, I was not able to confirm the status of the Holkotsgil gyrs. At any rate, this hypothesis did not explain why the Gaesadalur birds bred.

Seljadalur is about 5.5 km from both Dalfjall and Gaesadalur. If this distance were below the minimum territorial limit for Icelandic Gyrfalcons, one would expect to see at least some agonistic behavior, and I did not. In Alaska, Gyrfalcons have nested as close as 3.2 km, though the average is about 17 km (White & Cade 1971). In western Greenland the mean minimum distance between 7 sites was 7.8 km (Burnham 1975). Ernest Vesey found three cases of pairs of Gyrfalcons nesting within 4 or 5 km of each other in the western fjords of Iceland in 1936. All these sets of pairs laid eggs, one of the sets of pairs raised young, and at least one pair in the other two sets raised young. The fact that none of Vesey's nests were closer than 4 or 5 km, combined with (a) my finding of pairs residing at minimum distances of about 5.5 km, plus (b) the discovery of what appeared to be alternate sites or areas within 3 or fewer km of currently occupied sites, leads me to conclude that the minimum "psychological" distance between nesting pairs of Gyrfalcons in Iceland is between 3 and 5 km.

The most likely explanation for the nonbreeding at Myvatn in 1967 is probably the classical one. Ptarmigan populations over the whole of Iceland follow a well-defined ten-year population cycle (Gudmundsson 1960). Bengtson (1971) reported densities of breeding ptarmigan for the years 1961-1966 increasing from 1.7 to 7.4 per km² at Myvatn. According to A. Gardarsson (pers. comm.) and Bengtson (1971), 1966 was a peak ptarmigan year. Presumably the population of surviving Gyrfalcons in the spring of 1967 was at a peak, and the occupation of potential breeding sites at Myvatn was also at a peak. (This is one of the considerations that led me to define unoccupied, previously used nests 3 km or less from occupied nests as "alternative eyrie areas." If they were not "too close" to occupied nests, some should be occupied in a peak Gyrfalcon year.) However, the ptarmigan population had fallen in the spring of 1967 from the spring of 1966. Thus a relative lack of prey was probably the primary stress causing nonbreeding by Gyrfalcons at Myvatn in 1967. The tendency of the closer resident pairs, with (one assumes) smaller home ranges, not to breed would appear compatible with this hypothesis. At the same time the pair at Seljadalur had the additional stress of competing with a pair of ravens, and the pair at Vindbelgjarfjall may have been disturbed by the presence of immatures.

My interpretation of eyrie areas at Myvatn is rather speculative. Observation over an entire 10-year population cycle of the ptarmigan would be the only way of clarifying the situation. The status of the Seljadalur eyrie especially is problematic. Only observation over a period of years would determine whether it should be considered an independent area or an alternate to Gaesadalur. I would attach Seljadalur to Gaesadalur rather than to Dalfjall because the Dalfjall ridge contained several alternate sites while I only found one each in Gaesadalur and Seljadalur.

Literature Cited

- Beebe, F. L. 1960. The marine peregrines of the northwest Pacific coast. *Condor* 62(3):145–189.
- Bengtson, S.-A. 1971. Hunting methods and choice of prey of Gyrfalcons (*Falco rusticolus*) at Myvatn in northeast Iceland. *Ibis* 113:468–476.
- Brown, L., and Amadon, D. 1968. *Eagles, hawks and falcons of the world*, vols. 1, 2. New York: McGraw-Hill.
- Burnham, W. A. 1975. Breeding biology and ecology of the Peregrine Falcon (*Falco peregrinus*) in West Greenland. Master's thesis, Brigham Young University, Provo, Utah.
- Cade, T. J. 1960. Ecology of the peregrine and Gyrfalcons populations in Alaska. *Univ. Calif. Publ. Zool.* 63:151–290.
- Cade, T. J., and Weaver, J. D. 1976. Gyrfalcons-peregrine hybrids produced by artificial insemination. *J. N. Amer. Falconers' Assoc.* 15:42–47.
- Cramp, S., and K. E. L. Simmons (eds.). 1980. The birds of the western Palearctic. Oxford University Press, vol. 2.
- Dementiew, G. P. 1960. Der Gerfalke. Franckh'sche Verlagshandlung—Kosmos Verlag, Stuttgart.
- Gudmundsson, F. 1960. Some reflections on Ptarmigan cycles in Iceland. *Proc. Int. Orn. Congr.* 12:259–265.
- Hagen, Y. 1952. The Gyr-falcon in Dovre, Norway. *Skr. Norske Vidensk Akad. I. Math.-Nat. Kl. No. 4*, 1952:1–37.
- Jenkins, M. A. 1974. Behavior of the Gyrfalcons (*Falco rusticolus*) from hatching to fledging: a time-lapse photographic study. Master's thesis. Brigham Young University, Provo, Utah. 83pp.
- Lewis, E. (pseudonym of E. Vesey). 1936. In search of the Gyrfalcons. London.
- Platt, J. B. 1976. Gyrfalcons nest site selection and winter activity in the western Canadian arctic. *Can. Field-Naturalist* 90(3):338–345.
- Snyder, N. F. R., and J. W. Wiley. 1976. Sexual size dimorphism in Hawks and Owls of North America. *A.O.U. Monograph* #20.
- Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk* 83:423–436.
- Sutton, G. M. 1961. *Iceland summer: adventures of a bird painter*. University of Oklahoma Press, Norman.
- Wayre, P., and Jolly, G. F. 1958. Notes on the breeding of the Iceland Gyr-falcon. *Brit. Birds* 51:285–290.
- Weir, D. N. 1967. Possible source of error in raptor food analysis. *Bird Study* 14:194.
- White, C. M., and Cade, C. J. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. *Living Bird* 10:107–150.
- White, C. M., and Weeden, R. B. 1966. Hunting methods of Gyrfalcons and behavior of their prey (Ptarmigan). *Condor* 68(5):517–519.



Figure 3. View from the lip of Dimmuborgir into the depression. The photo does not give an adequate idea of the depth or the extensiveness of Dimmuborgir. In the distance some of the hills that form the eastern boundary of the Myvatn basin. In the foreground low bushes of birch (*Betula pubescens*). May 1967.



Figure 4. View of Hrossaborg from the road across the Burfellshraun. The Gyrfalcon eyrie is on the opposite side. Note the sparsely vegetated "sandy waste." In the distance are the mountains of the Central Highlands of Iceland. June 1967.