MEDDELELSER OM GRØNLAND
UDGIVNE AF
KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND
BD. 205 • NR. 3

GREENLAND PEREGRINES AT THEIR EYRIES

A BEHAVIORAL STUDY OF THE PEREGRINE FALCON

BY

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WITH 6 FIGURES

KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI A/S
1975

Abstract

Two families of the endangered peregrine falcon *(Falco peregrinus tundrius)* were observed at their nest cliffs in West Greenland. This article describes the breeding behavior of the tundra peregrine, including vocalizations, prey species, feeding and hunting, activity cycles, parental roles, and inter- and intraspecific behavior.

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ISBN 87 421 0117 4

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Introduction

The peregrine falcon *(Falco peregrinus)* is a large, swift hawk nesting on inaccessible cliff ledges throughout most of the world. As one would expect of a species found all the way from the Arctic to the Tropics, individuals vary considerably from one portion of the range to another, and a dozen or more subspecies are recognized (HICKEY & ANDERSON, 1969). WHITE (1968) included most of West Greenland as a breeding area for the newly described subspecies *F. p. tundrius*. These tundra peregrines are morphologically distinct from *F. p. anatum*, found through most of temperate North America, and are highly migratory, unlike their more southerly cousins.

This paper reports on our observations of the peregrine falcon at the nest cliff in Greenland. In 1972 we watched one family intensively for most of a six week period from June 23 to August 3. In addition we observed a peregrine family at a second cliff from July 22 to 24, and in 1973 returned to the second cliff for observations from July 26 to August 5. Our conclusions on peregrine behavior are based primarily on the falcons at the first location, supplemented with our notes from the second nest cliff. Although BENT (1938), PROCTOR (1947–48), HALL (1955), CADE (1960), HERBERT & HERBERT (1965), and FISCHER (1968) among others have also reported on peregrine behavior at the nest, or eyrie, only CADE watched the arctic peregrines, and his work was done in Alaska, an environment somewhat different from that of West Greenland. We compare our observations of the Greenland falcons with the present knowledge of the peregrine as presented in the literature.

The peregrine has been intensively studied in the last twenty years because of the rapid decline and disappearance of its populations through much of North America and Europe. Evidence points to chlorinated hydrocarbons such as DDT and dieldrin as the major cause of the decline (HICKEY & ROELLE, 1969). These hard pesticides collect in the fat tissues of animals and become heavily concentrated in the peregrines and other predators at the tops of food chains. Though the doses are not usually lethal in the peregrine, they inhibit deposition of calcium carbonate during eggshell formation (RATCLIFFE, 1967). This results in thin, weak eggshells which the incubating adults often break, causing a lowered

reproductive success. Until recently arctic populations of peregrines in North America appeared healthy and unaffected by these pesticides (HICKEY, 1969), but now thin eggshells, pesticide residues, and reproductive failures have been noted in Alaska and portions of northern Canada (CADE *et al.*, 1968; CADE & FYFE, 1970).

The Greenland peregrines have not escaped the effects of pesticides used far to the south. We ran our study in conjunction with a breeding survey of Greenland peregrines performed by WILLIAM G. MATTOX, WILLIAM A. BURNHAM, and, in 1972, RICHARD A. GRAHAM. Reproductive success remained high in both 1972 (MATTOX *et al.*, 1972) and 1973 (BURNHAM *et al.*, 1974), but in 1972 the contents of two eggs were found to contain moderate levels of DDE and eggshell fragments were 14% thinner than Greenland eggshells collected before 1940 (WALKER *et al.*, 1973).

We hope that documenting the behavior of the *tundrius* peregrines will serve two main purposes. First, comparison will become possible between this subspecies in its distinctive environment and peregrines in other areas. In particular, prey and feeding habits on the breeding grounds may explain why Greenland peregrines remain reproductively healthy while other populations, even in the Arctic, vanish. Second, our study may contribute to a more thorough understanding of the processes by which the hydrocarbons cause reproductive failure. As the Greenland peregrines already hold pesticide concentrations, they cannot safely be considered a normal, unaffected population. Yet comparisons, between our data and future observations of arctic peregrines from populations suffering reproductive failure, may reveal disruptions in behavior caused by high hydrocarbon doses that contribute to the species' demise.

Field methods

In this paper we shall refer to the two study sites as the first and second eyries. We do not know if the same adults formed the pair at second eyrie in both 1972 and 1973. Unless otherwise specified, second eyrie observations refer to the 1973 family.

In 1972 CLEMENT and HARRIS occupied a base camp below a large cliff within hearing and sight of the first eyrie. The six-week study period ran from two weeks before the peregrine eggs hatched to one and a half weeks before the young fledged. Altogether we recorded 231 hours of direct observation. Most notes were taken from a site on the cliff about 100 yeards away from and level with the eyrie. A spotting scope was used which gave a good view of the eyrie and scrape (nest). Until the eyasses (nestlings) were a week old, we visited the scrape on warm days for a fifteen-minute period every four to six days. We also watched from

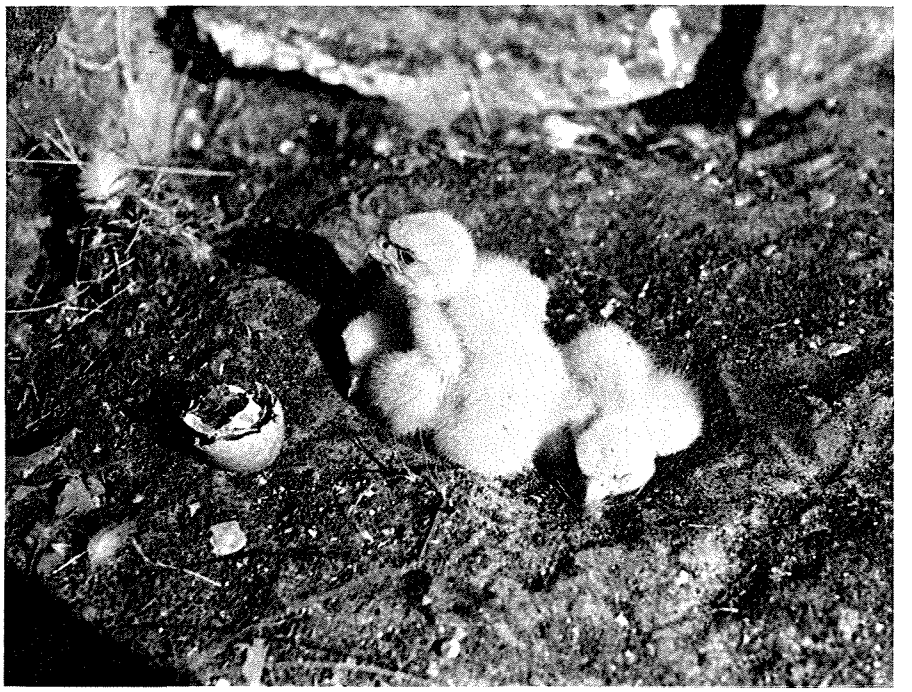

Figure 1. Three peregrine eyasses, aged 4 days, huddle in the shallow scrape. Notice the eggshell fragments which were collected and later measured.

the tent and other areas. During the second week after hatching, CLEMENT constructed a blind on the eyrie ledge thirty feet from the scrape. Observations and pictures were taken from the blind. A 200-foot fixed rope provided access to the eyrie.

Our observations covered several 24-hour periods as well as shorter daytime periods. We took detailed notes on development of the young, care of young and eggs, intra- and interspecific behavior of the adults, feeding, hunting, prey species, weather conditions and diurnal activity cycles. HARRIS made a census of the prey population in the area of the eyrie cliff. Prey remains and castings were collected for analysis.

When we arrived in late June, the adult pair were incubating four eggs, all of which hatched before mid-July. Unfortunately, the last-hatched, a male, died at the age of three weeks. We discovered its body on our last visit to the eyrie on August 12, at which time the three surviving eyasses, two males and a female, were less than a week from fledging.

We briefly visited the first eyrie in 1973 and found three eyasses (see Figure 1).

In 1973 HARRIS camped alone beneath the second eyrie cliff, from the time the eyasses were about one week old until they were $2^1/_2$ weeks

old. He set his two-man tent on the hill rising opposite the cliff, 250 yards away from but nearly level with the eyrie, so that the young could be seen in the scrape. He observed the family for a total of $93^1/_4$ hours and noted the same range of activities as in the 1972 study, but did not erect a blind. He climbed to the nest ledge itself only once. In 1973 this second eyrie held three eyasses. On August 5, when the eyasses were closely examined and banded, all appeared healthy and likely to fledge.

In 1972 the second eyrie held four eggs; but by August 4 only one sickly looking eyass remained in the scrape. During our brief observation period at this location in 1972 both authors took notes for a total of $21^1/_2$ hours, when the eyass and any still living siblings were newly hatched. We watched from our two-man tent set up one hundred yards from the cliff base.

On all occasions the very real possibility of permanently scaring away incubating adults, or of cooling and killing egg embryos or young was avoided by carefully limiting the length of disturbance times.

The Eyrie Locations

The two peregrine eyries were located 10 miles apart in central West Greenland. Greenland is covered by a great inland icecap that leaves only a narrow strip of ice-free land along most of the island's outer edges. Our two eyries were located 75 and 85 miles from the outer coast, at a latitude where the ice-free land has a total width of approximately 100 miles. The two are representative of the nine eyries found in the 1972 and 1973 surveys (data on the nine eyries will be published at a later time), and probably of inland eyries generally. Fewer peregrines nest on the outer coast than inland (SALOMONSEN, 1950–51) and these coastal falcons experience different conditions because of cooler, wetter weather in summer and the availability of sea birds as prey.

The first eyrie was located on a southwest-facing rock cliff which reached a maximum height of 700 feet (214 m). The eyrie was about 1,150 feet (350 m) above sea level and overlooked a valley with a small lake, two brooks and an associated marsh. The vegetation consisted mainly of grasses, mosses, and, in sheltered places, bushes usually less than two feet in height. Three miles west of the cliff was a large lake. The eyrie and scrape were located about 200 feet (61 m) up from the base of the cliff (i.e., top of the talus) on one end of a 100-foot long (30.5 m), 3-foot wide (1 m) ledge. The scrape lay under a 2-foot overhang of rock. From the eyrie, one had a commanding view of over ten square miles (26 km^2) of tundra to the southwest.

The second eyrie cliff reached a maximum height of 120 feet (37 m) and faced south-southeast. In 1973 the eyrie was 80 feet (24 m) up from

the cliff base, at an elevation of 800 feet (244 m) above sea level; its ledge was 10 feet (3 m) long, 3 feet (1 m) wide. It overlooked tundra of an appearance similar to that surrounding the first eyrie, but had a much less extensive view. Fifteen or more small lakes lay within two miles (3 km) of the cliff, but most of them were out of sight of the eyrie. Above the scrape a 25-foot (8 m) wall rose, slightly overhung, before the cliff top receded into grasses. In 1972 the scrape was on a ledge 40 feet (12 m) from the cliff base, exposed at a protruding part of the cliff with no overhang above.

Both first and second eyries overlooked valleys particularly lush and sheltered. The ledges held thick grasses. In 1972, we unwisely removed much of the grass to enhance our view from the blind. The frequently overheated young we then observed suggested that the intense sun at these latitudes is a problem. At age $3^1/_2$ weeks these eyasses moved down the ledge away from the scrape to reach the shade of undisturbed grass.

Vocalizations

Many studies have described the important vocalizations of the peregrine falcon (HEATHERLEY, 1913; HAGAR, *in* BENT, 1938; CADE, 1960; HERBERT & HERBERT, 1965; FISCHER, 1968), but little work has been done to interpret their use and meaning. We recognized three basic calls. The call used most often, and under the most varied conditions, was "kaaa-kaaa-kaaa". There was some graduation between this and the next most frequently used call, "kak-kak-kak-kak". The second had many short staccato syllables while the first had drawn out syllables, usually no more than three or four. The third basic call, least often used, was "clee-chip" often repeated several times or during feedings abbreviated to "chip ... chip ...".

At the first eyrie the "kaaa-kaaa" call was given by either adult while it was perched on the cliff. No particular event seemed to elicit it. And the other adult usually did not respond, except that the female would call immediately before the male returned to the cliff area with prey, apparently answering his distant "kaaa-kaaa's". Shortly before the actual exchange of food, both adults would shift to the "kak-kak-kak" call. Both uttered this latter call continuously when we visited the scrape or when they chased ravens intruding near the cliff. They used the "clee-chip" call twice when a stranger peregrine visited the cliff. Otherwise at first eyrie we heard it at the very moment of food exchange between adults, or more quietly while the female fed the eyasses (neither of the other calls was used at feedings), while twice the male uttered it as he left the scrape after incubating the eggs, and once as he soared before the cliff.

The second eyrie falcons were generally quieter than the first pair. But when used their calls followed the patterns we have noted for the first pair. The second male was a silent bird. Except for one occasion when he may have given the first call, he made no sounds at all except aggressively towards human intruders and once a gull near the cliff, when he gave the "kak-kak" call. The female uttered the first call at food exchanges or sometimes when alone she flew before the cliff. Only her "kaaa-kaaa's" sounded at food exchanges. Often "clee-chip's" or "chip's" came from the eyrie when she fed the young, and once as she shifted position while brooding. At the start of one feeding one of the three eyasses squatted two feet to the left of the scrape; as the female stood over the other two, she looked at this third eyass, and called "clee-chip". When the eyass showed no interest in parent or food, the female turned back towards the scrape and fed the waiting two. Perhaps this call is used to attract the eyasses' attention.

In 1972 the second eyrie male did give the first and second calls when with the female at the cliff, following the usage described for the first eyrie male.

The seemingly contradictory use of the "clee-chip" call in times of aggression as well as during feeding has led to varied interpretations in the literature. HAGAR (*in* BENT, 1938) described it as a conversational note used between mates on the cliff, "presumably ... a pleasing sound," while CADE (1960) suggested it was connected with an aggressive tendency between the male and female. Its association with the otherwise aggressive "kak-kak-kak" call during food exchanges supports CADE's hypothesis. FISCHER (1968) thought the "clee-chip" call was used during times of maximum excitement, thus during either aggression or food exchanges. We noted the "clee-chip" call only in intra-specific situations, and its use at the very instant of food exchange agrees with FISCHER's suggestion. At the second eyrie twice after food exchanges and once as we walked at the cliff top the female's cries at their shrillest broke into two syllables, resembling the "clee-chip", and thus suggesting that the third call is a more intense version of, but closely related to, the first two calls. However, use of the call during the 5-minute feedings, and its absence during our presumably highly threatening visits to the scrape, render an excitement hypothesis less satisfactory.

Reliance on Sight

Several episodes demonstrated that these arctic peregrines rely almost entirely on sight in their perception of threat. On our visit to the second eyrie in 1972 the very aggressive pair started calling as soon as

we came within sight of their cliff perches. The mile of terrain between us and the peregrines contained three small valleys lying perpendicular to our path. As we entered each valley, we dropped out of sight of the eyrie and the peregrines would stop calling. But upon topping each ridge, the calling would start up again. Even if one of the falcons was flying overhead, when we dropped *out of sight of the eyrie*, it would stop calling and return to the cliff. A similar event repeatedly occurred when a person climbed the fixed rope to the first eyrie. If we hid behind a rock, out of view of the falcon, it would quiet down and cease to appear aggressive. The unimportance of sound and smell (HEATHERLEY, 1913) further point out the reliance of these birds on sight. In the blind one could sneeze or even softly whistle without causing alarm to an adult peregrine thirty feet away.

To man the blind we both climbed to the eyrie and, after one entered the blind, the other would leave the ledge and cliff area. However, it may be possible for a single person to enter the blind without another's assistance as a distraction. We believe that once the observer is no longer visible the peregrines will cease to recognize danger and will resume normal activities.

Few investigators have realized the extent of the peregrine's reliance on sight. Could it be that the unobstructed vision in the continual daylight of the tundra has heightened this reliance? If that is the case, then the falcons of lower latitudes would depend less heavily on sight for identifying enemies. This question needs more study to be answered.

Breeding Timetable

As we were not present for a full season either summer we must extrapolate the partial data we collected to get a complete timetable for the breeding cycle at our two eyries. Three of the young at the first eyrie hatched between July 6 and July 9, and the runt male probably on July 13. About thirty-five days later, on August 12, we noted that these eyasses would not fledge for several more days. At the second eyrie we observed one eyass and two eggs on July 19—thus at this eyrie hatching occurred ten to thirteen days later in the season than at the first eyrie. We estimate that the eyass at the second eyrie in 1972 did not hatch until about July 22.

Other studies of the peregrine in the Arctic have shown that the full breeding cycle takes approximately ninety-five days. Courtship is short in the Arctic, lasting only about one week as compared to two or three months in California (CADE *et al.*, 1971). Incubation probably lasts twenty-nine days (CADE, 1960), although some studies in temperate areas have

found longer incubation periods, even up to thirty-nine days (HALL, 1955). The time between hatching and fledging (first flight) has been estimated to extend anywhere from thirty days (CADE *et al.*, 1971) to forty days (R. A. GRAHAM, unpublished data). Three to four weeks after fledging the young start making successful hunts. This dramatic transition to independence climaxes several weeks of unsuccessful hunting attempts. Soon after their first successful hunt, the young falcons become independent and leave their parents.

Working from this timetable we calculate that the first eyrie falcons arrived at their cliff in late May. At this time temperature averages were near 1 to 2°C for this part of Greenland (Weather Bureau, 1972). The eggs must have been laid during the first week of June with average daily temperatures around 5°C. The eyasses would be ready to start the southward migration in the second half of September. The second eyrie families were two, and $1^1/_2$ weeks behind this schedule. These dates agree with the Greenland observations of SALOMONSEN (1950–51) and with the passage of migrating peregrines in mid-September and October off the Maryland coast (WARD & BERRY, 1972).

The breeding cycle appears to have a significant relationship with the breeding cycles of the falcon's prey. The majority of their prey is migratory, and arrives in Greenland about the same time as the peregrine (SALOMONSEN, 1950–51). The young falcons are hatching out just as the prey species begin to fledge. We saw the first fledged wheatears *(Oenanthe oenanthe)* on July 2, redpolls *(Carduelis flammea)* on July 12, lapland longspurs *(Calcarius lapponicus)* on July 14, and snow buntings *(Plectrophenax nivalis)* on July 15. The hatching of the falcons also coincided with the onset of the passerine moult. Whether these relationships are coincidental or not, their result is obvious. Fledgling passerines are a far easier prey to catch than adult passerines, and they probably comprise the bulk of the diet of a peregrine family. CADE (1960) found that the prey and falcon cycles were similarly correlated in Alaska.

Role Behavior

There were pronounced roles for each adult of the first eyrie peregrines. The male was the primary foodgetter, bringing in 112 of the 133 meals consumed on the cliff. The female incubated the eggs except for brief periods while she ate food the male brought, and six times when the male relieved her at the scrape; he incubated seven of the first $40^1/_2$ hours we observed the first eyrie. Except for the last of these times, on July 10, when we believe three of the four eggs had hatched, we never observed the male brooding the young. The female brooded them, always fed them,

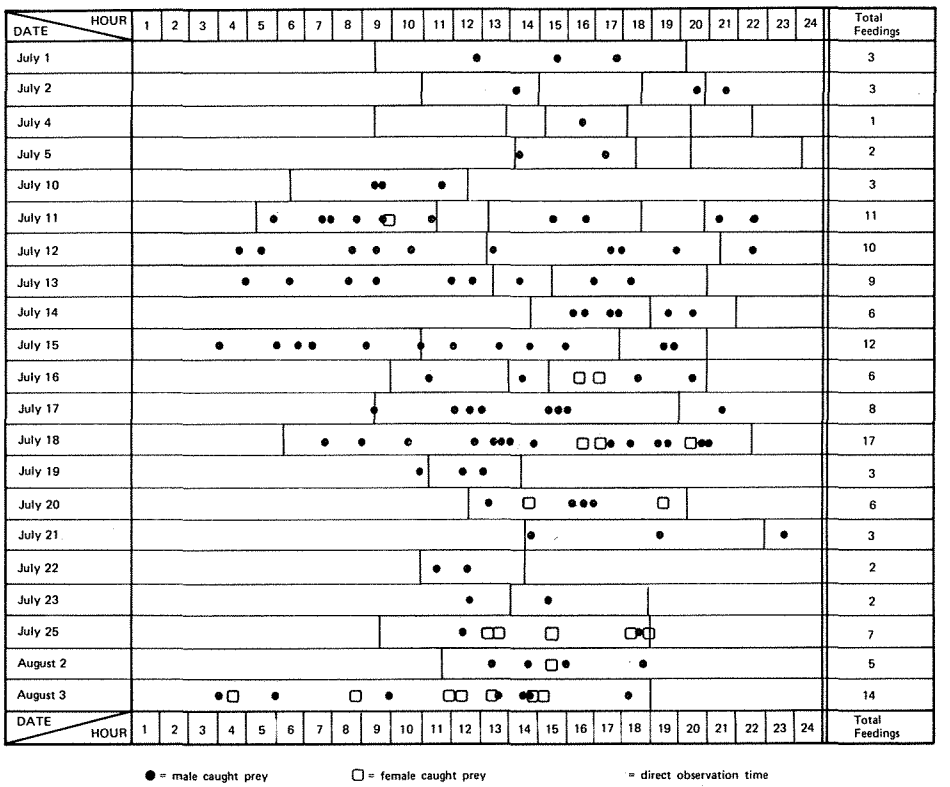

Figure 2. Schedule of Successful Hunts and Feedings.

watched over them. The male sometimes perched on the eyrie ledge or would stand at the scrape. As can be seen from Figure 2, he performed almost all hunting for female and young until two weeks after hatching, when the female assumed her share of the burden.

During the time when the female was obliged to incubate or brood, the male was the most active defender of the cliff area. If the male was present at the cliff he usually made the first aggressive flights and stoops against intruders. Only when the male was gone did the female assume the full role of territorial defender. Whenever we approached the scrape the male would stoop closer to us than the female, but the female would remain more consistently overhead. She would be the first to return to the ledge after our departure. From two weeks after hatching, when the female began to hunt away from the cliff area, the young were left entirely unguarded for increasing periods.

We noticed similar differences between the adults at the second eyrie, although both members of that pair were more aggressive than the adults at the first eyrie. At the first eyrie, the female attacked ravens several times; at the second eyrie, the male handled all raven intruders alone.

While normally the adults cooperated with no sign of antagonism, after hatching several incidents revealed that the female was clearly dominant over the male. Much of her dominance was exhibited right at the scrape or on its ledge, an area which the female seemed to consider as her own territory. After hatching, the female would rarely allow the male near the eyrie, except to drop off food. Several episodes from our notes clearly illustrate this point. When the young were about a week old, the female flew to a perch away from the scrape. The male (without prey) then flew in from far away, landed on the eyrie ledge and started to walk towards the scrape. Immediately the female dropped down to the eyrie ledge and screamed the aggressive "kak-kak" call at the male until he flew away. Later, the male was flying within five feet of the eyrie ledge, about to land when the female gave several "kaaa-kaaa" calls. The male instantly veered off and did not land at the eyrie. Delay in obtaining food may have caused several instances of female aggression. If the male returned to the eyrie with no prey after a long absence, the female would scream "kaaa-kaaa" and even "kak-kak" calls at him for as long as ten minutes. Then he would usually fly away and return several minutes later with food. Once we witnessed a similar occurrence when the male did not go off on an early morning hunt, as was his custom. FISCHER (1968) has suggested that the female is able to demand food from the male.

Another example of female dominance during the post-hatching period was occasionally evident when the male brought food to the eyrie ledge. The female would crouch over the prey, with wings drooped and tail spread, calling "kaaa-kaaa" until the male left, and only then would she feed the young.

The first male, therefore, was not welcome in the eyrie and scrape. Once, when the young were several weeks old, he was standing at the brink of the ledge after having dropped some food (the female was away). The largest of the eyasses finished its eating and charged straight towards the male, who called "kak-kak" at the young falcon and promptly flew off.

The pair relationship at the second eyrie closely resembled that of the first eyrie pair. The female performed almost all brooding. The male provided food for the family. Of the ninety-two prey bodies brought to the cliff, the female at most may have caught two or three. Several times at feedings friction between the pair was apparent. Once as he returned to the cliff with food the male landed not at the eyrie but at another ledge, and the female immediately landed beside him, bumped him from his perch and followed him for a food exchange in the air. While sometimes the male stood by the scrape for several moments after a food exchange, and once he fed the eyasses a passerine body closely following a feeding by the female, always the male would fly when the female returned from her perch elsewhere on the cliff, and at times she in landing would force him to move.

Figure 3. The female falcon pauses in her feeding to look out over the tundra.

The size difference between the adults—females are approximately one-third larger than the males—contributes to female dominance (CADE, 1960). Sexual dimorphism in size may also allow differential niche utilization, as SELANDER (1966) and STORER (1966) have proposed. Though the female may concentrate on larger prey in regions where there is a greater variety available, we could distinguish little difference between male and female prey utilization. Rock ptarmigan *(Lagopus mutus)*, small ducks and northern phalarope *(Phalaropus lobatus)* are the only larger prey available to peregrines in the survey area. The female brought in one of the two ptarmigan seen eaten at the first eyrie (see Figure 3). We discovered the other ptarmigan after it was delivered to the cliff, so we could not determine which adult caught it. The ptarmigan population in the survey area was extremely low in 1972. Though we saw little difference in birds caught by male or female, the female may concentrate on larger prey in summers of higher ptarmigan densities.

The Daily Cycle of Activity

The peregrine falcon is a diurnal bird. We were interested in the timetable of its activities in the continual daylight of the Arctic and shall discuss hunting and feeding, incubating and brooding, and flying.

Hunting and feeding were the most prominent aspects of the falcons' time budget. Figures 2 and 4 summarize the observed frequency of these

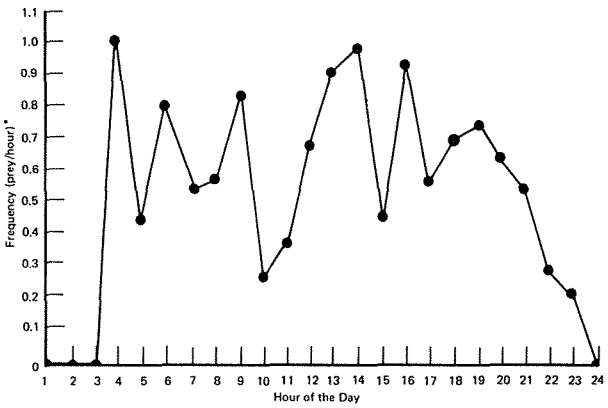

Figure 4. Daily Hunting and Feeding Cycle.

activities at first eyrie. In preparing these data it was necessary to define a relationship between hunting and feeding. Since 133 of the 135 instances of feeding we observed in the cliff area occurred with freshly-killed prey brought in by a hunting adult (the remaining two feedings were on food cached on the cliff), we have concluded that almost every feeding by an adult or young on the cliff corresponded to one successful hunt. Therefore, each dot on Figure 1 designates a successful hunt followed by a feeding at the cliff. We could not ascertain the number of feedings by an adult away from the cliff. Therefore the figures in Figure 1 provide a low estimate of total hunts and feedings for the first eyrie family, especially late in the season when the female as well as the male left the cliff for long periods.

The diurnal activity cycle of the peregrines was patterned much like that of their prey. Like the small passerine birds the falcons were most active in the early morning and mid-to-late afternoon. No appreciable activity, including hunting, feeding, or flying occurred between 2100 and 0300 hours of each day. The lighting during this "night" period could best be described as early dusk, sufficient for any activity the falcons wished to engage in. But prey species were inactive during this time, and not until the morning sun hit a section of tundra did the birds residing there become very active. The peregrines began their first morning hunts towards that part of the tundra which received the earliest sunlight. In lower latitudes, the active day is significantly shorter (FISCHER, 1968) due to the longer night period.

As long as the eggs needed incubation or the young needed brooding, the female would be at the scrape all night. The male always spent the night perched on the cliff in the vicinity of the eyrie. Only occasionally would either adult fly or call at night.

The male would give prey to the female either on the eyrie ledge or while both adults flew. As can be seen from Figure 2, our observations suggest that the number of feedings was greatest in the early morning and early afternoon, with a lull at mid-morning and the frequency declining in late afternoon. Other studies (HICKEY, 1969; WHITE & CADE, 1971) hinted at this but did not present any quantitative data. The feedings were rarely spaced evenly. Frequently, there would be two or three separate kills brought to the cliff within half an hour, then a two or three hour lull would occur until the next feeding. We observed feedings as often as seventeen times a day and estimated feedings at the cliff averaged twelve to fifteen a day after hatching. Feedings noticeably increased after July 10 (see Figure 1) when the eggs hatched. In 1972 when the second eyrie held only one eyass we observed feedings less frequently. But in 1973 we estimate the male brought in sixteen to twenty meals a day. The frequency of feedings at second eyrie declined after 1900 hours as the evening progressed, and the latest feeding was observed at 2256 hours.

At first eyrie incubation and brooding were important activities until about two weeks after the young had hatched. The longest period the eggs were left unattended was twenty minutes. After hatching, the female brooded the young almost constantly until they were about a week old, at which time she began leaving them alone if the sun was warm. These periods gradually lengthened until at two weeks after hatching the female only went near the young during the cold night and for feeding. For these first two weeks the female left the eyrie for short hunts at the base of the cliff, or for a few minutes of leisurely flying in front of the cliff. When the sun was warm and she was not brooding, she would stand at the edge of the eyrie, preening, sleeping or gazing off into the tundra. By $3^1/_2$ weeks after hatching, she did no brooding even at night and frequently left the cliff area altogether.

The female at the second eyrie kept very close to the scrape until the eyasses were two weeks old. Because weather was cold (temperatures about 5 to 10°C) during their second week, she brooded more constantly than the first female had. But during the sunny third week she frequently sat out on the ledge or perched elsewhere, and occasionally left the cliff for brief periods. The eyasses moved out from the scrape onto the ledge to preen or squat.

This female, like the first female, would occasionally lean over the ledge in a grazing posture—body low and head stretched forward—to pluck at the dirt. These motions may have simply served to pass the time; we doubt that she was cleaning her beak, for they did not accompany preenings or follow feedings. When away from the eyrie ledge the female usually perched at one of several ledges and rock points on a protruding part of the cliff below and forty feet west of the eyrie. The characteristics

of the cliff do affect the adults' behavior. The second male perched much less often on the cliff than did the first male on his cliff. For the smaller cliff did not have the sweeping breadth of view, and the male frequently perched on boulders or small ledges on higher parts of the hill. For this reason Harris could never spot him during the inactive night period.

Weather strongly affected the extent of the adults' flying at first eyrie. Bad weather with precipitation and low clouds kept both adults sitting on the cliff much of the day. We noted that when cold, rainy, or snowy weather set in, the clouds frequently formed a layer resting on top of the landforms, including the occupied cliff. It may be that the peregrines placed their eyrie low to escape this cloud layer.

When the weather was warm and clear, the male would spend most of the day away from the cliff (presumably flying). At intervals he would return for a few minutes with food, then soar away again. But he always returned to spend the night. Unlike the peregrines HERBERT & HERBERT (1965) observed near New York City, he did not seem to prefer a particular night perch. As both adults easily caught passerines near the cliff during bad weather, it is likely that these long flights by the male were spent largely in leisurely soaring, and not serious hunting.

Prey, Hunting and Feeding

The vast majority of the first eyrie peregrines' prey consisted of passerines, four species of which lived in the area: lapland longspur, snow bunting, redpoll, and wheatear. Rock ptarmigan and northern phalarope constituted the remaining small portion of their diet. The only small mammals available as prey for these Greenland peregrines are young arctic hares *(Lepus arcticus)*, but we found no fur traces at any time. It was difficult to determine the species of prey from observation because the small passerines, especially after plucking, looked identical. And we could seldom use leftover prey for identification because the peregrines immediately ate all they caught. Only once was food found in the first eyrie, and only twice did we see it cached on the cliff. Consequently, castings were collected for prey analysis.

The sample castings and prey remains we collected from several different eyries were analyzed by ROXIE LAYBOURNE of the Bird and Mammal Laboratories, U.S. Fish and Wildlife Service. She identified twenty-six separate food items, belonging to the following species:

lapland longspur *(Calcarius lapponicus)*	10
snow bunting *(Plectrophenax nivalis)*	9
redpoll *(Carduelis flammea)*	2

wheatear *(Oenanthe oenanthe)*	1
rock ptarmigan *(Lagopus mutus)*	2
northern phalarope *(Phalaropus lobatus)*	2

Lapland longspurs and snow buntings dominated the sample. In agreement with this result, at the second eyrie we observed only passerine-sized prey at the scrape.

A breeding bird census was made of a one-third square mile rectangle in the valley immediately beneath the first eyrie. We counted the following:

lapland longspur	22 pairs
wheatear	7 —
snow bunting	5 —
redpoll	4 —

Our rectangle contained more willows and rocks than much of the tundra and thus a greater density of prey than average over the whole survey area. Similarly the second eyrie had particularly favorable habitat about its base. The abundance of lapland longspur may well explain the fact that it was commonly preyed upon by the peregrines. The few ptarmigan and phalarope kills probably resulted from the relative scarcity of these two prey species. We found a low density of breeding ptarmigan, phalarope, and oldsquaw *(Clangula hyemalis)* in the survey area.

The prey analysis does show that the peregrines will prey upon almost anything in the right size range. This agrees with data from other studies. RATCLIFFE (1969), for example, cited 142 prey species in Great Britain. But the significant point is that these peregrines of inland Greenland, whether because of choice or prey availability, fed primarily on the four passerines. Three of these species (all but the wheatear) winter in northern areas where they primarily eat seeds (BENT, 1968). At present MATTOX and BURNHAM, members of the breeding survey run concurrently with our study, are analyzing Greenland specimens of these species for pesticide residues. Low concentrations of DDT and the other chemicals in its summer prey might explain the continuing health of inland Greenland's peregrine population.

CADE and others (CADE, 1960) have suggested that a commensal relationship exists between prey species nesting near the cliff and peregrines, where the peregrines' defense of the eyrie also serves to protect the other birds from predators. Other falcons and ravens may have avoided the first eyrie cliff, but arctic foxes *(Alopex lagopus)* lived at the cliff base, and the peregrines themselves posed a major threat. Several times at both eyries we did see a snow bunting hopping on the same ledge with a peregrine, sometimes within two feet of the falcon. Neither the falcon

nor the bunting took much notice of each other, and the falcon never attacked in this situation but only when the bunting was farther away and flying. But contrary to a belief sometimes expressed in the literature on raptors, that hawks do not hunt immediately around their nests, we generally found that passerines near the cliff were as likely to be taken as those farther away. In fact at the first eyrie, in bad weather the closer the prey, the more likely the peregrines were to hunt it. Often the female on the eyrie ledge watched the passerines below, and sometimes she stooped upon one directly from her perch. Similarly both adults at the second eyrie hunted below the cliff. Probably the peregrines ignored the buntings because they were already satiated, or because the prey was so close that the falcon would have little chance of catching it with its typical aerial pursuit. Disadvantages for the passerines of inhabiting a peregrine cliff certainly outweighed the advantages.

While often the males soared high into the air, we never saw either male pursue prey from the lofty flight in the manner that observers in temperate regions have noted (HALL, 1955; HERBERT & HERBERT, 1965). Instead the adult of either sex would fly low and swiftly over the tundra. Passerines were pursued close to ground level. The following from CLEMENT's notes is a typical example of what we saw. In this case the falcon had spotted motion from her eyrie ledge perch.

> Noiselessly, the female made a long shallow dive straight at a single spot on the tundra. The dive lasted about five seconds. As she neared the ground, she braked and swerved, then went forward after what I saw to be a passerine. The passerine cut back, and the female followed it until the passerine landed and stayed in a clump of bushes. Twice the female flew up twenty feet and dove on the bushes without getting the passerine to come out. She then flew back to the eyrie.

This time the falcon failed, but the same type of hunting strategy was observed to be successful. These hunting scenes suggest that the falcons try to scare a passerine into the air and then chase it. Yet at other times we observed the falcon glide away after only one unsuccessful stoop at a flying passerine. The absence of trees in Greenland to interfere with flight low over the ground, and the tendency for three of the four passerines (all but the redpoll) to fly low, probably account for differences in hunting methods between Greenland peregrines and those falcons to the south.

Bad weather with its low cloud level altered the hunting pattern of the first eyrie peregrines. During such weather, both adults remained near the eyrie. Most hunting was directed towards prey at the base or sides of the cliff and very little time was spent in securing it. The second eyrie cliff, being smaller, did not offer as many hunting opportunities,

Figure 5. The female peregrine returns from her hunt with a large prey item, probably ptarmigan. Notice the flies on the huddled eyasses.

and the male usually left its immediate vicinity to hunt. We do not know whether he wandered less far in bad than in good weather.

We witnessed an activity for which we found no description in the literature. Five times at the first eyrie one of the adult falcons flew down into the valley, landed, spent several minutes leisurely hopping around on the ground, and then flew back. Once the adult brought back prey, and once the hopping occurred at the precise spot where, several minutes before, the adult had made a kill. This suggests that the hopping is part of a hunting pattern. It may be that the adults were looking for ground caches, although twice we visited the scenes of kills soon after the kill, and nothing remained but down and a few feathers. We doubt that peregrines would have hidden previously killed prey in such exposed spots where foxes prowl. It is more likely they were looking for a bird hidden in the low bushes, or possibly they sought passerine young that had not yet fledged. We never observed hopping behavior at the second eyrie, but once the male darting low just over bushes landed on the ground. The passerines were chipping in alarm. He flew, immediately to land again, and after a moment he took to the air with prey in his talons.

During the second week of the eyasses' lives, the first eyrie female would sometimes hunt in the immediate vicinity of the cliff. About two weeks after hatching (July 21), the female began to go off and hunt on her own away from the cliff (see Figure 5). Three times the male and fe-

male left the cliff area together: once they returned together without food; the other times they returned separately, the last time each with food. At the second eyrie the female was first observed hunting on August 4, when the eyasses were two weeks old.

The second eyrie male brought slightly more food to his mate than did the first male. Because there were only three eyasses to feed rather than four, the female cached more food than did the first eyrie female, part or all of nine out of the ninety-two meals the male brought to the cliff. Similarly, she retrieved four (not the same) caches, while the male fetched one from a ledge also.

At both eyries the female's behavior as the male returned to the cliff with food usually determined whether the food exchange occurred on the eyrie ledge or in the air. At the second eyrie if she was sitting low on the scrape the female apparently would not notice the male until he landed on the ledge, perhaps because of his silence. But if she sat out on the ledge or stood alertly looking from the scrape, she usually would fly calling "kaaa-kaaa" to meet the male in the air before the cliff. At the first eyrie, where the male vocally announced his return to the cliff, the sitting female was more likely to leave the scrape for an aerial exchange.

At the second eyrie the male did not always follow the female's lead in determining the type of food exchange. Twice he briefly circled before the cliff while the female waited on the ledge, until she took to the air to meet him. Twice he flew past her to land on the ledge, and she immediately followed to snatch the prey.

Only in bad weather did the first eyrie male eat at the cliff. At other times he kept both the female and the young supplied with food, but ate his own away from the cliff. For the first two weeks, the female shredded all meat for the young. Towards the end of this period the young started moving about on the ledge. On July 25, $2^1/_2$ weeks after hatching, the eyasses attempted to seize food from each other or snatched at the body, which the female held. At about this time the female began catching as much food as the male. Feedings lasted three to six minutes, and though there was some crowding and jostling, all four young were fed well. They usually lined up for the female to feed them. Occasionally, one or two young would not get much, especially if they were in the back row, but at another feeding, these would be in the front. Even the ill-fated male eyass was not deprived. When all the young except the runt could feed themselves (August 2) there was little fighting over meat when either adult would drop its prey on the ledge and leave. One of the young would seize the body and eat undisturbed by the others. Yet the female still fed the eyasses several times on August 3 (see Figure 6).

This raises the question of why the small male at the first eyrie died. When last observed, the eyass appeared healthy, though considerably

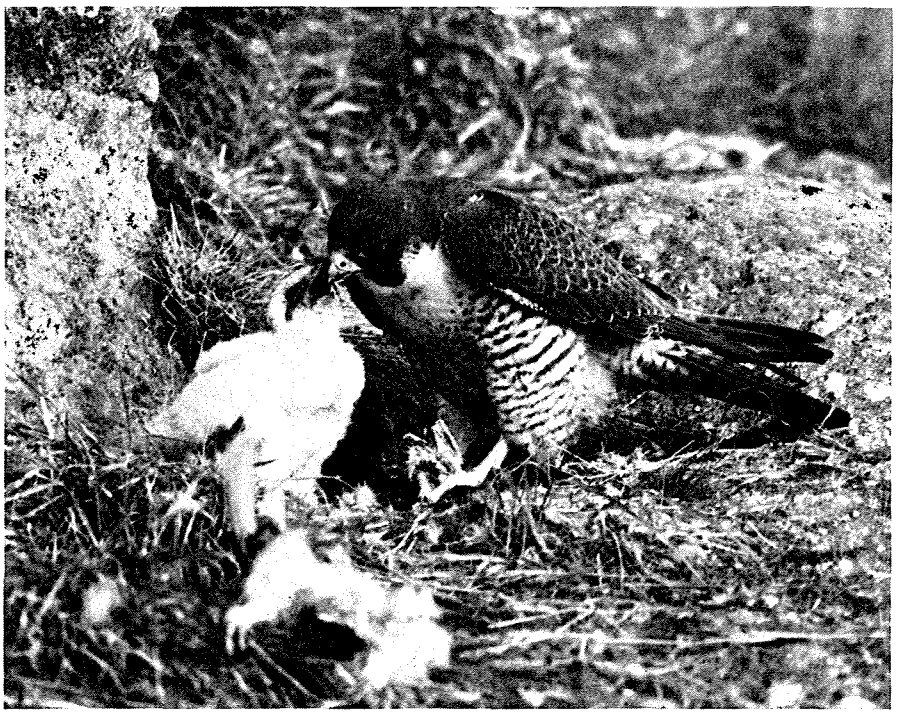

Figure 6. The female feeds shredded meat to the littlest eyass, aged $2^1/_2$ weeks. The other eyasses have moved up the ledge among grasses that provide shade.

smaller and less developed than its siblings. A week later it was found dead in the scrape. BURNHAM and GRAHAM estimated it had been dead three days. Several possible causes of death for an eyass do not seem to apply in this case. Man, ravens, and arctic foxes are the only predators on young peregrines in the survey area. But the dead eyass did not appear physically harmed. Chilling was unlikely as the weather was excellent at the time of death. We found no evidence of disease, although this remains a possibility.

The most likely cause of death was the little male's inability to feed himself or at least to compete with his siblings when the female stopped shredding and distributing the meat. The larger young began picking at the prey and eating large chunks long before the runt male. The female adult probably stopped feeding all the young at the same time. The stronger eyasses took passerines the adults brought to the ledge, and the underdeveloped male died of starvation. This type of starvation has a behavioral basis and is not related to food resources or hunting success.

HEATHERLEY (1913) also witnessed starvation in peregrine eyasses which he thought was a behavioral phenomenon. Other studies have indicated that starvation is not necessarily related to food supply or

hunting success. The ease with which peregrines catch prey when they are seriously hunting is well documented (CADE, 1960; HICKEY, 1969). Instances have been noted where a single male was able to feed himself and incubate a clutch of eggs to successful hatching (HAGAR, 1969). Because peregrines are generalists and prey upon most small and medium-sized bird species, starvation in peregrines does not seem to result even when prey densities are low (RATCLIFFE, 1969). The first eyrie adults appeared to have no difficulty with catching prey. On rainy days, when they hunted near the cliff, their hunts were successful almost half the time. And on several occasions the male brought in two separate prey items within a ten-minute period. However, food shortages may cause death of the young at eyries at higher elevations or in the coastal regions where the tundra is barren and prey scarce. We do not know why only one eyass survived at the second eyrie in 1972 after four eggs had been laid, although we noted that the exposed ledge offered little protection from the weather.

Defense of the Eyrie

Eight times we witnessed peregrine aggression towards ravens at the first eyrie. Only when the raven was perched on the cliff or flying near the eyrie cliff did the peregrine attack seriously enough to inflict injury (none of these attacks actually caused injury). The falcons did not stoop on a raven flying beyond three hundred yards from the nest. When a raven passed at a greater distance they might only watch or else fly over it, calling but not attacking. This pair was always more tolerant of humans than of ravens, and usually did not call, never flew or stooped upon us until we climbed to the cliff base itself directly below the eyrie.

At the second eyrie the male attacked ravens seven times. His pursuit of the intruders was far more violent than that of the first eyrie pair. His flight assumed a pendulum motion, with the raven at the bottom of each stoop. The raven at the instant before the blow would thrust its feet before the peregrine, although the male rising out of his stoop would sometimes strike from below. Frequently it took shelter on the eyrie cliff or hill above it, where the peregrine attacks would increase in vigor and trap the raven among boulders, once for fifteen minutes after the male had stooped on it seventy or eighty times. The ravens would first come under attack about 300 or 350 yards from the eyrie. Even during these incidents the male remained silent, and only raven croaks and rattles could be heard.

The second female never assisted the male against ravens. But once a white-winged gull (either Iceland, *Larus leucopterus*, or glaucous, *Larus hyperboreus*) approached the cliff. The male's attacks were much fiercer than against ravens; both peregrines gave their aggressive call, and as the

gull neared the cliff, the female stooped on it also. Directly before the eyrie she grappled with it, and the two fell a dozen feet before she released her hold. Both adults followed the gull away from the cliff, the female soon returning but the male pursuing for seven hundred or more yards into the next valley.

This pair also was more aggressive towards the observing team than the first eyrie pair. The male once called and flew out to circle over us when we were one-half mile away. Sometimes the male or female would cry "kak-kak-kak" when HARRIS moved outside his tent, 250 yards away. Their aggressiveness made observation more difficult than at first eyrie. In 1972 the second eyrie pair was still more aggressive. In both years we used the tent as a blind for observation. But while the second pair reacted to human approach more quickly than to the raven's, the adults never stooped on us except at the cliff itself, and never came closer than a dozen feet from our heads.

The falcons at both eyries made moderate adjustments to continued human presence. In both summers as the observing period passed the falcons would show fewer aggressive responses, and not react as quickly when we approached the cliff.

Although the first eyrie was less than two miles (3 km) from another peregrine eyrie, we witnessed only two instances of intra-specific aggression between the first eyrie peregrines and an alien, adult peregrine. A strange adult once landed on the cliff, and this prompted extremely aggressive diving attacks accompanied by "clee-chip" calls from both the resident peregrines. These attacks and pursuit lasted until the group was about one-third mile from the cliff, at which time the resident peregrines returned to their cliff. Later in the summer, an alien peregrine soared high over the cliff. The resident male flew up quickly with "kak-kak" calls, made several swoops on the alien, then escorted it away until about one-half mile from the eyrie. These territorial attacks were more aggressive and extended farther from the eyrie than any of that pair's attacks on ravens or humans.

CADE (1960) differentiates three parts of a peregrine's breeding territory: an area immediately around the eyrie which is always vigorously defended, a larger area which is usually defended, though less vigorously, and then a large expanse of tundra beyond the cliff which is used for hunting and in which no territorial aggression takes place. The size of these three concentric areas varies with the aggressiveness of the breeding pair. The behavior of our two pairs towards all intruders was consistent with CADE's model, although we do not know how the falcons reacted to other peregrines on the hunting range. The minimal aggression between the first eyrie falcons and the pair nesting only two miles distant suggest that hunting ranges are modified to exclude the vicinity of neighbouring eyries and thus allow use of cliffs in close proximity without excessive conflict.

Future Research

Many aspects of peregrine behavior at the eyrie in Greenland still need to be described. In particular we lack observations during courtship and post-fledging periods, and we do not know how activities and diet of coastal pairs differ from those of peregrines inland. Future observations of Greenland peregrines would reveal consistencies and variations in behavior among peregrine pairs. A timelapse photographic study, using the techniques of ENDERSON, TEMPLE, & SWARTZ (1972), in conjunction with observations and blind work would provide more continuous data on events at the scrape.

Continuation of this study as well as the population survey in Greenland will allow correlation of changes in peregrine behavior with altering levels of pesticide contamination. Similarly, detailed observations should be taken of arctic peregrines from an already declining population. Contrasting these results with our data may reveal the presence of disturbances in behavior, perhaps a key factor in reproductive failure.

Acknowledgements

We wish especially to thank Dr. WILLIAM G. MATTOX, Lt. Col. RICHARD A. GRAHAM, and WILLIAM A. BURNHAM, our companions in the field, for their help at all stages of the study. Without them we never could have worked in Greenland. The United States Air Force, the Richard King Mellon Foundation, and Dartmouth College supported our work. Our research was performed in close cooperation with Dr. FINN SALOMONSEN, Curator of Birds, University Zoological Museum, Copenhagen, Denmark. ROXIE LAYBOURNE of the Bird and Mammal Laboratories, U.S. Fish and Wildlife Service, provided valuable analytical aid. We are grateful to J. J. HICKEY, S. W. MATTESON, and J. E. Ross for commenting on drafts of this paper.

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Added in proof:

BURNHAM, W. A., M. A. JENKINS, F. P. WARD, W. G. MATTOX, D. M. CLEMENT & J.T. HARRIS. 1974: Falcon Research in Greenland, 1973. *Arctic*, 27(1): 71–74.

Færdig fra trykkeriet 19. decbr. 1975