

## Natural History of the Gyrfalcon in the Central Canadian Arctic

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**ABSTRACT.** A population of breeding gyrfalcons was studied from 1982 to 1986 on a 2000 km<sup>2</sup> area in the central Arctic of the Northwest Territories. Each year 14-18 territories were occupied. The mean inter-nest distance was 10.6 km, giving one of the highest recorded densities for the species. There was a tendency for regularity in spacing of territories. Most (85%) nests were in abandoned stick nests of common ravens or golden eagles. Rough-legged hawk nests were not used by gyrfalcons, despite numerous available. Mean date of initiation of laying was 8 May. Mean size of clutch was 3.80 and of brood was 2.53, and mean productivity was 1.50 fledged young. A reduction of 48% from estimated number of eggs laid to number of fledglings was determined. Reproductive success declined with increased severity of spring weather, notably increased days and amount of precipitation.

**Key words:** gyrfalcon (*Falco rusticolus*), natural history, reproductive ecology, central Arctic

**RÉSUMÉ.** Entre 1982 et 1986, on a étudié une population de gerfauts en reproduction dans une zone de 2000 km<sup>2</sup> dans la région centrale arctique des Territoires du Nord-Ouest. Quatorze des 18 aires étaient occupées chaque année. La distance moyenne entre les nids était de 10,6 km, soit la plus grande densité relevée pour cette espèce. Les aires avaient tendance à être espacées régulièrement. La plupart des nids (85 p. cent) étaient situés dans des nids de brindilles occupés précédemment par des corbeaux communs ou des aigles dorés. Bien qu'ils aient été largement disponibles, les nids de buses pattues n'étaient pas utilisés par les gerfauts. La date moyenne du début de la ponte était le 8 mai. La taille moyenne de la couvée était de 3,80, et celle de la nichée de 2,53; la productivité moyenne était de 1,50 oisillons emplumés. On a calculé qu'il y avait une diminution de 48 p. cent entre le nombre estimé d'oeufs pondus et le nombre d'oisillons. Le succès de la reproduction diminuait quand le climat printanier était plus rigoureux, en particulier quand le nombre de jours de précipitations et le montant des précipitations augmentaient.

**Mots clés:** gerfaut (*Falco rusticolus*), histoire naturelle, écologie de la reproduction, région centrale arctique

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**Реферат:** Популяция размножающихся кречетов изучалась от 1982 г. до 1986 г. на площади размером в 2000 км<sup>2</sup>, находящейся в центральной Арктике Северо-западных территорий Канады. Птицы занимали от четырнадцати до восемнадцати территорий ежегодно. Среднее расстояние между гнёздами равнялось 10,6 км, что является одной из самых высоких известных плотностей для этого вида. Наблюдалась склонность к регулярности в расстояниях между территориями. Большинство (85%) гнёзд находилось в гнёздах (из палок), брошенных обыкновенными воронами или орлами-беркутами. Кречеты не использовали гнёзд мохноногих канюков, несмотря на то, что таких гнёзд было много. Средней датой начала яйцекладки было 8 мая. Среднее количество яиц равнялось 3,80, средний выводок равнялся 2,53, а среднее число птенцов, оперившихся на каждой занятой территории равнялось 1,50. Было определено, что по сравнению с примерным количеством снесённых яиц, количество оперившихся птенцов было ниже на 48%. Степень успеха размножения понижалась за счет повышения суровости весенней погоды, а именно, за счет увеличения периодов и количества осадков.

**Важные слова:** кречет, *Falco rusticolus*, естественная история, репродукционная экология, центральная Арктика.

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## INTRODUCTION

The natural history of gyrfalcons (*Falco rusticolus*) has been studied in the Palearctic from the U.S.S.R. (Kishchinskii, 1957; Dement'ev, 1960), through Scandinavia (Hagen, 1952; Langvatn and Moksnes, 1979), Finland (Pulliainen, 1975) and Iceland (Bengtson, 1971; Nielsen, 1986). Distributional and biological studies of the species have occurred in Greenland (Jenkins, 1974; Burnham and Mattox, 1984) and in North America, including Alaska (Cade, 1960; Roseneau, 1972) and the Yukon (Platt, 1976, 1977; Mossop, 1980; Barichello, 1983). The Northwest Territories (N.W.T.) contain enormous expanses of potentially excellent gyrfalcon habitat (Cade, 1982), yet only in recent years have studies of distribution and productivity been undertaken (Bromley, 1983; Bromley and McLean, 1986). Prior to 1980, studies were local in nature, of short duration or ancillary to other research objectives. Some information is available from the interior tundra of the central N.W.T. (Kuyt, 1980), the Western Arctic (R. Fyfe, pers. comm. 1984), Ellesmere Island (Muir, 1975) and northwestern Hudson Bay (Calef and Heard, 1979). Yet little is known thus far about the basic ecology of the species in the N.W.T.

From 1982 to 1986 we examined a high-density population of gyrfalcons at the Kilgavik study area in the central Canadian Arctic (Fig. 1), several hundred kilometres from previous sites of gyrfalcon research. Research on the study area was initiated in 1982 (Bromley, 1983). Relative ease of access enabled a number of sites to be monitored regularly throughout the breeding season. We examined distribution and density of breeding pairs, food habits, nest site selection, nesting behaviour, causes of egg and nestling mortality and productivity. Information was also gathered on sympatric nesting raptors, the golden eagle (*Aquila chrysaetos*), tundra peregrine falcon (*Falco peregrinus tundrius*) and rough-legged hawk (*Buteo lagopus*), as well as the common raven (*Corvus corax*).

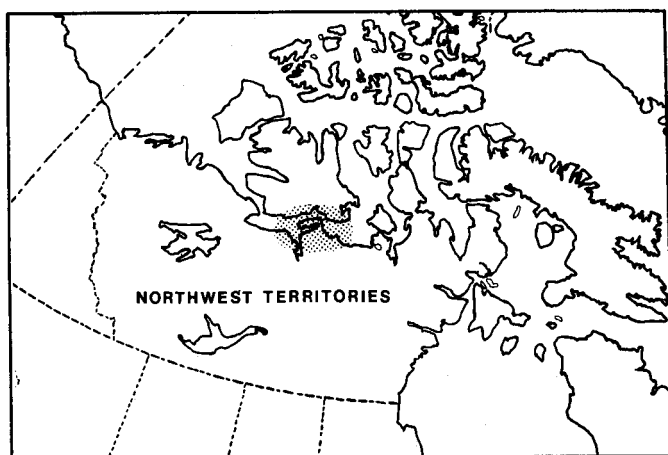


FIG. 1. General location of the Kilgavik study area (shaded).

## STUDY AREA

The study area, approximately 2000 km<sup>2</sup> of rugged mainland tundra, lies within 20 km of the coast along the southeast side of Melville Sound and Elu Inlet (centred at 68°10'N, 106°15'W) and includes some islands in these water bodies (Poole, 1987).

The boundaries of the study area were defined mainly with geological features; toward the limits of the area cliffs diminish and the topography becomes rolling or flat. Granitic intrusions and diabase dykes and sills form the main geological features of the area (Fraser, 1964). The diabase formations, lines of cliffs or circular blocks of rock rising above the surrounding terrain, provide nesting ledges facing in most directions. Elevations range from sea level to 375 m.

The flora consists of wide-ranging, low-arctic tundra species (Porsild and Cody, 1980). *Carex* spp., cotton-grass (*Eriophorum* spp.) and lichens and mosses predominate in moist areas. Willows (*Salix* spp.), dwarf birch (*Betula glandulosa*), Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*) and bell heather (*Cassiope tetragona*) are the dominant vascular plants. Fifty-three species of birds and 17 species of mammals were recorded on the study area (Poole, 1987). There are no permanent human inhabitants, although Inuit sporadically hunt, fish and trap in the region during the winter.

January and July mean daily maximum temperatures are -30° and 10°C respectively; precipitation varies from 100 to 150 mm annually (Maxwell, 1980). The land is snow covered for about 260 days of the year, with snow-melt usually beginning in mid- to late May. Sea ice usually persists until the second or third week of July. Weather data from Cambridge Bay, 140 km northeast of the centre of the study area, were used to examine the effects of late winter-early spring conditions on the chronology of the gyrfalcon annual cycle. While the Kilgavik region averages slightly warmer conditions than Cambridge Bay, weather systems appear to affect both areas similarly.

## METHODS

Surveys for raptors at Kilgavik were initiated in July 1982 (Bromley, 1983). Because the researchers were unfamiliar with the area and no spring surveys were undertaken in 1982, we excluded that year from some of the analyses. We conducted intensive studies of gyrfalcons at Kilgavik in May and the first week of June in 1983 and 1984, during the first 2 weeks of July and August of 1984, and from early May to early to mid-August 1985 and 1986. A week was spent on the study area in late March and early April 1986.

To avoid confusion, we provide the following definitions of terminology used:

- Territory — an area containing one or more nest sites within the range of a pair of actual or potential breeders (Postupalsky, 1974).
- Nest site — the actual site of the nest. More than one nest site may be present within one territory, being used in different years. Nest sites within 3 km of each other are considered alternatives, unless evidence indicates separate territories.
- Occupied territory or nest site — a territory or nest site where a single bird or a pair of birds is present at some time during the breeding season, although eggs may not be present. The presence of eggs may be inferred by a bird in incubation posture on the nest.
- Productive territory — a territory within which a minimum of one chick is raised to an advanced stage of development (at least 25 d old) and is known or assumed to have fledged.
- Production — the total number of young fledged or raised to an advanced stage of development from all productive territories.

- Productivity — a rate expressed as the mean number of known or assumed fledged young per occupied territory.

Snowmobile surveys were conducted each spring until early to mid-June. Previously located raptor nest sites were checked, and all cliffs capable of supporting raptors were systematically examined to locate new sites. Most sites were checked at least twice in the spring and often more frequently; thus it was unlikely that we missed territorial or nesting birds. In support of this, we discovered no new territories during July helicopter surveys in areas that had been examined by snowmobile. Arrival dates of all migrants were noted, as well as other indices of spring phenology.

To determine the chronology of the gyrfalcon breeding cycle the following assumptions were made: the laying interval was 48 h (P. Trefry, pers. comm. 1985); incubation began with the penultimate egg (Platt, 1977); the incubation period was 35 d (Cade and Weaver, 1976); and the fledging period was 47 d (Jenkins, 1974; this paper). Hatch date was observed (three sites in 1985, four sites in 1986) or calculated by back dating from the estimated age of nestlings (Poole, 1988a). The sex of each nestling was determined late in the nestling period when size dimorphism was obvious.

From early to mid-June, access to sites was on foot, by helicopter (Bell 206B Jet Ranger) and by boat along the coast following breakup of the sea ice in July. From 12 to 16 h of helicopter surveys were flown each July from 1982 to 1986 to census the study area, visit all gyrfalcon sites and band nestlings. Notes were taken on the nature of the nest substrate (ledge, old or new stick nest; identity of builder), nest aspect, percent overhang above nest and nest and cliff height from bottom (details in Barichello, 1983).

Nest sites were observed for a total of 801 h to document nesting behaviour. Observations were made from distances of 200-400 m using 7x binoculars and 20x spotting scopes and were conducted throughout the field season. Gyrfalcons appeared to habituate rapidly to the presence of observers.

Time-lapse 8 mm movie cameras (Temple, 1972) were set up at three gyrfalcon nest sites in 1985 and four in 1986. At each site, one frame was exposed every 3 min to provide a sampled documentation of behaviour at the nest. Each roll of film provided 1 wk of coverage. A frame interval of 6 or 9 min was selected in instances where access to the site was not possible on a weekly basis, such as during spring thaw. The films were analyzed in an 8 mm film editor (MKM Industries, Inc., Model 824). Of over 118 000 exposed frames, 3.1% were unusable because of darkness or inclement weather. Unit malfunction caused the loss of 2 wk of film, and exposure problems prevented midday analysis of some rolls of film from one site in 1985, eliminating 37% of the frames exposed at that site.

To determine the density of nesting pairs, we calculated the average distance between each nest site of occupied territories (mean internest distance; Ratcliffe, 1980), such that no distance was measured twice (i.e., 15 distances from 16 sites). As a second method, we used the mean internest distance as the radius for a circle of territorial influence, drawn around the outermost nesting pairs, to provide a hypothetical boundary to the study population (Ratcliffe, 1980).

The GMASD test (geometric mean, arithmetic mean square distance; Brown, 1975) was used to evaluate the spatial distribution of gyrfalcon territories each year. Three territories located on islands in Elu Inlet were excluded from calculations. The GMASD test is the geometric mean of all internest distances

divided by the arithmetic mean of these distances. GMASD values below 0.65 indicate random distribution; values above 0.65 denote regular spacing increasing to perfect regularity at a value of 1.0 (Nilsson *et al.*, 1982).

Weather parameters from 21 April to 30 May were examined in relation to laying dates, brood size and production of gyrfalcons. These dates cover the period during which weather may have the greatest impact on a breeding pair, from about 2 wk prior to laying to two-thirds through incubation.

Statistical tests follow Sokal and Rohlf (1981). Differences among data sets were considered significant when  $p \leq 0.05$  ( $p$  — probability), unless stated otherwise.

## RESULTS

### Density

Twenty-one gyrfalcon territories were located during the course of the study, with 14-18 occupied each year. The mean internest distance between occupied nest sites at Kilgavik ranged from  $9.5 \pm 5.4$  (SD — standard deviation) km in 1983 to  $11.4 \pm 4.3$  km in 1985. Actual nearest neighbour distances ranged from 1.0 to 20.0 km. The average mean internest distance from 1983 to 1986, 10.6 km, was used to calculate a study area size of 4450 km<sup>2</sup> by Ratcliffe's (1980) method. Approximately 1350 km<sup>2</sup> of ocean were included in the above estimate; its removal reduced the study area to 3100 km<sup>2</sup>. Using this conservative value as the area encompassing the population studied, we calculated a density for all territories located during the study of one territory · 150 km<sup>-2</sup> and an annual average of one occupied territory · 190 km<sup>-2</sup>. Eliminating tracts of land and ocean far (>10 km) from any gyrfalcon nest sites resulted in a study area of 2000 km<sup>2</sup> and densities of one territory · 95 km<sup>-2</sup> for all territories and an annual average of one occupied territory · 125 km<sup>-2</sup>.

Spacing of territories was fairly regular in the contiguous portion of the study area in most years (1984, GMASD value 0.87; 1985, 0.76; 1986, 0.74) but randomly spaced in 1983 (0.49). A value of 0.74 was obtained when all territories occupied from 1983 to 1986 were considered.

### Nest Sites

Thirty-four different nest sites were used for 59 nesting attempts. Most sites were nests built by ravens (62%) or golden eagles (23%) (Fig. 2). Two sites (6%) were stick nests of uncertain origin and three sites (9%) were ledges with no stick substrate. In 1984, 19 nests built by ravens and 31 built by golden eagles were located; thus selection by gyrfalcons for raven nests was evident ( $X^2 = 14.6$ ,  $p < 0.01$ ). Some of the nest sites were occupied alternately by gyrfalcons and ravens or golden eagles. Mean brood size of gyrfalcons in nests built by golden eagles was similar to that in nests built by ravens (1.94 vs. 2.03, Mann-Whitney Test  $U = 386.0$ ,  $p = 0.77$ ). In several instances freshly built raven nests were usurped by gyrfalcons. We saw no evidence of gyrfalcons taking over nest sites currently occupied by golden eagles.

The mean cliff and nest height of all nesting attempts was  $24.5 \pm 9.8$  m and  $12.9 \pm 6.5$  m respectively and ranged from a nest at a height of 4 m on a 16 m cliff to one 30 m from the base of a 45 m cliff. Mean overhang was 81%, with most nest sites (68%) covered by a complete overhang and only five sites (15%) with less than 50% overhang. Nest sites used by gyrfalcons faced in all directions, with no one direction pre-



FIG. 2. Female gyrfalcon at a 1.2 m high nest built by golden eagles. This site was occupied by gyrfalcons all five years of the study and was productive four years. (Photo by R. Bromley.)

ferred ( $X^2 = 5.06$ ,  $p > 0.5$ ). The number of nests with a southerly (SE through SW) versus northerly (NW through NE) aspect was similar, 12 and 13 respectively. Mean brood size (in this case the mean number of young fledged, including sites that failed) differed, with 1.59 young produced on southerly and 2.35 young on northerly oriented sites; the difference approached significance (Mann-Whitney Test  $U = 500.0$ ,  $p = 0.08$ ).

Nine sites were located on cliffs adjacent to the ocean; hence nest sites ranged in altitude from near sea level to about 215 m above sea level. Only 10 sites were accessible to humans without full climbing gear, and only a few sites appeared to be accessible to mammalian predators such as foxes (*Vulpes vulpes* and *Alopex lagopus*) and wolverines (*Gulo gulo*).

The average number of known alternative nest sites within each territory was  $1.7 \pm 0.9$  and ranged from one to three. Gyrfalcons usually switched nest sites each year, but in some territories the same nest was used year after year. Most alternative sites were located within 1 km of one another on the same cliff or occasionally on adjacent cliffs. The greatest distances between alternatives were 4.8 and 3.2 km, with the alternatives located along linear features, in these cases a valley and a line of cliffs along a lake respectively. The sites 4.8 km apart were considered alternatives because both sites were never occupied in the same year, and the peculiarities in plumage colour of the pair using the sites each year were identical.

#### Winter Occupancy

All 21 territories were visited during the late winter survey. Eight territories had evidence of use (fresh excrement or prey remains and pellets). Gyrfalcons were observed at six of these territories. Lone males were seen at four sites and pairs were observed at two. Probably some birds were missed because of their skittish nature at this time. Of the eight sites occupied in early April, seven were occupied later in spring (May) and eggs were produced at six sites.

Based on accumulation of excrement relative to snow layering at and below winter roosts (Cade, 1960; Platt, 1977; Barichello, 1983), gyrfalcons had been present since at least February, and ravens since early March, but there was no

evidence for continuous occupancy by either species throughout the winter. The first golden eagle was sighted on 2 April.

#### Spring Phenology

Late winter-early spring weather varied greatly, from a cold spring in 1983, which broke eight 40 yr daily minimum temperature records for May, to a warm, dry spring in 1984, with temperatures many degrees above normal (Table 1). The weather in the spring of 1985 was mild but wet. In 1986 normal temperatures occurred but fierce storms prevailed. The weather in May 1986 was particularly severe, as three major storms, with winds of up to 70 kph and driving rain, freezing rain and snow pellets, battered the area for a total of 9 d. The poor weather in 1986 continued well into June; 50% snow-free ground was attained on 2 June in 1983, 15 May in 1984 and 19 May in 1985, but because of snow accumulation during storms, not until 18 June in 1986. Although there was a significant difference among years in arrival dates of migrants (Kruskal-Wallis 1-way ANOVA,  $X^2 = 14.9$ ,  $p < 0.01$ ), only 1983, with its extremely low temperatures, was significantly later than the subsequent 3 yr (Duncan Multiple Range Test,  $p < 0.05$ ).

TABLE 1. Mean temperature, number of days of snow and total precipitation for late April and May, Cambridge Bay, N.W.T., 1983-86<sup>a</sup>

	1983	1984	1985	1986	40-year mean
21-30 April T <sup>b</sup>	-19.4	-15.1	-18.5	-17.3	-17.2
P <sup>c</sup>	2(4)	0(Tr)	2(4)	1(16)	
1-10 May T	-20.3	-7.5	-10.1	-12.5	-13.3
P	2(8)	0(Tr)	3(68)	2(13)	
11-20 May T	-17.2	-6.9	-1.4	-8.8	-10.8
P	2(6)	0(Tr)	5(32)	1(12)	
21-30 May T	-8.5	-5.0	-1.6	-7.2	-6.0
P	3(40)	0(Tr)	5(20)	6(201)	

<sup>a</sup> Unpublished data from Arctic Weather Centre, Atmospheric Environment Service, Environment Canada, Edmonton, Alberta.

<sup>b</sup> Mean temperature (°C).

<sup>c</sup> Number of days with precipitation (amount of precipitation in mm).

#### The Incubation and Nestling Period

There was a significant difference between years in the initiation dates of laying in gyrfalcons (Kruskal-Wallis Test  $H = 13.0$ ,  $p < 0.01$ ). Median date of clutch initiation was earlier in 1984 and 1986 than in 1983 and 1985 (Fig. 3). No relationship was found between median laying date and weather parameters examined from 21 April to 30 May each year. The spread in laying dates ranged from 6 d in 1985 to 30 d in 1983, with the mean of yearly median laying dates being 8 May. Summing all years, we found that most pairs (86%) started laying by 15 May. Hatch dates ranged from 1 to 30 June (mean 15 June), with most young fledged, after a nestling period of about 7 wk, by late July to early August.

A mean clutch size of  $3.80 \pm 0.52$  eggs was obtained for 20 nests over the course of the study (Table 2). A clutch of four was by far the most common, found in 85% of nests. Two clutches of three and one of two eggs were also observed. Not included in the above calculations was a renest with a clutch of three (Poole, 1988b).

Because of sexual dimorphism of plumage colour, the sex of the adult incubating or brooding could be easily identified from

TABLE 2. Breeding success of gyrfalcons on the Kilgavik study area, 1982-86

	1982	1983	1984	1985	1986	Mean <sup>a</sup>
No. of occupied territories	11	18	15	14	17	16
No. of pairs laying (%)	10(91)	15(83)	12(80)	9(64)	13(76)	12.3(77)
Mean clutch size (no. of nests) <sup>c</sup>	—	3.3(4)	4.0(6)	3.8(5)	4.0(5)	3.80(20)
No. of pairs producing young (%)	9(82)	12(67)	11(73)	9(64)	9(53)	10.3(64)
No. of pairs fledging young (%)	9(82)	11(61)	11(73)	9(64)	7(41)	9.5(59)
Production	—	25	31	20	20	24
Mean brood size, successful pairs	—	2.27	2.82	2.22	2.86	2.53 <sup>b</sup>
Productivity	—	1.39	2.07	1.43	1.18	1.50 <sup>c</sup>

<sup>a</sup> The 1982 data were not used because no spring surveys were conducted.

<sup>b</sup> 1-way ANOVA  $F=1.40$   $df=3,34$   $p=0.26$ .

<sup>c</sup> 1-way ANOVA  $F=1.14$   $df=3,60$   $p=0.36$ .

time-lapse photography. The colour phase of adults observed each year approached a 1:1 ratio (63 grey:65 white). Thirty-one (55%) of the 56 pairs observed were composed of adults of different colour. Half (28) of all pairs, including 5 of the 7 being filmed, were grey male:white female pairs and only 5% were white male:grey female pairs.

Male participation in incubation varied among pairs. At site 112 in 1985 (the only site where a camera was in place prior to hatch) the male participated in 26% of the last half of incubation. Summing direct observations, we found that for all sites males incubated 24% of the time in 1985 ( $n=119$  h, 3 sites) and 17% in 1986 ( $n=41$  h, 4 sites).

Of seven sites monitored at hatch, six broods hatched within 48 h, and the seventh in 72 h. Evidence of greater asynchrony in hatching, based on differences in weight and plumage development, was observed at several sites where there appeared to be a spread of up to 6 d in the estimated age of siblings.

Nearly continuous brooding (>80% of time-lapse frames each day) took place at most sites until the chicks were 10-13 d old, although at one site in 1985 nearly continuous brooding persisted until the chicks were 19 d old. In 1986, all brooding terminated

when the chicks were 16-21 d old; in 1985 some brooding (<20% of frames each day) at two sites persisted until 31 and 32 d.

Participation by males in brooding ranged from 5 to 25% (mean 13%,  $n=1142$  h, 4 sites). No relationship between the time spent brooding and brood size or weather was apparent to explain the differences in division of brooding by sex among sites. In one pair the male brooded 5.0% of the time in 1985 and 4.8% in 1986.

Fledging dates were obtained for 11 nestlings of known age. Males fledged at 45-47 d of age (mean 46.0 d,  $n=7$ ), 2-3 d earlier than females (mean 48.3 d, range 47-50 d,  $n=4$ ) because of differential allocation of resources into body size and feather development (Fig. 4).

The sex ratio of nestlings during 1984-86 varied from predominantly females (1984, 11 males:18 females) to predominantly males (1985, 14:6) to nearly even (1986, 9:11). The ratio in 1985 approached significance ( $X^2=3.2$ ,  $p=0.07$ ). However, the combined 3 yr ratio ( $n=69$ ) was even (34:35,  $p>0.9$ ).

Although mean brood size and productivity varied among years, the differences were not significant ( $p>0.25$ , Table 2). The mean brood size from 1983 to 1986 was  $2.53 \pm 0.89$  young, while productivity averaged  $1.50 \pm 1.43$  young. No correlation was found between laying date and brood size on a within-year basis ( $p=0.26-0.49$ ). When laying dates from all years were combined, the relationship approached significance ( $p=0.06$ ), but

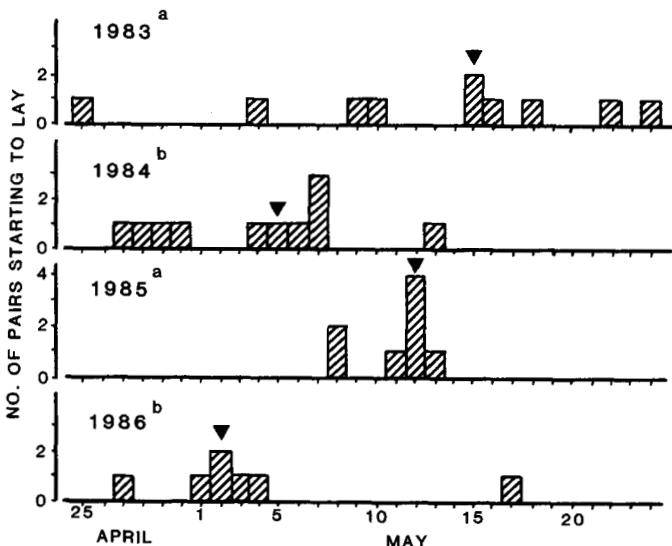


FIG. 3. Dates of initiation of laying by gyrfalcons at Kilgavik, N.W.T., 1983-86. Triangles indicate median date. Years superscripted with unlike letters differed based on Duncan Multiple Range Test ( $p<0.05$ ).



FIG. 4. A 42-d-old nestling female gyrfalcon (left) and her 43-d-old male sibling. Note the differences in head size and shape and feather development. (Photo by K. Poole.)

the correlation remained weak ( $r = -0.27$ ). Annual mean brood size also was not correlated with either April-May or June weather variables. In 1986, the year with the lowest productivity, the highest mean brood size was attained. Total annual production ranged from 20 to 31 young.

Spring weather apparently influenced production of young. Production was negatively correlated with the number of days that snow fell ( $r = -0.93$ ,  $p = 0.04$ ) and with total precipitation ( $r = -0.86$ ,  $p = 0.07$ ) from 21 April to 30 May. Mean temperature alone had little influence on overall reproductive performance ( $r = 0.02$ ,  $p = 0.49$ ).

Failure to lay had a major influence on productivity; 15 of 64 pairs (23%) occupying sites did not initiate a clutch. Pairs that failed at some point in the breeding cycle were seldom seen on subsequent visits to the territory.

Using the terminology of Mearns and Newton (1984), territories were considered as either "regular" or "irregular," depending on their history of occupancy. Regular territories ( $n = 9$ ) were those used three or more times in the 5 yr of the study; irregular territories ( $n = 12$ ) were occupied 1 or 2 yr. Only 6 (29%) of the 21 territories were occupied every year, and of these only 4 (19%) were always productive. The regular territories accounted for 74% of total production; however, there was no significant difference in productivity between territories used regularly and irregularly (Mann-Whitney Test  $U = 506.5$ ,  $p = 0.14$ ).

#### Egg/Nestling Mortality

Summing data from 1983 to 1986 (Table 2), we assumed 3.8 eggs was the mean clutch size for all pairs laying eggs (49 pairs), for an estimate of 186 eggs laid. Since total production over the 4 yr was 96 fledglings, a 48% reduction occurred.

The exact causes of mortality were difficult to pinpoint. Total clutch or brood loss occurred in 11 nests; however, only one clutch loss and two brood losses were actually observed. All three losses occurred in 1986, resulting from severe spring weather. The clutch loss was a consequence of freezing rain and snow virtually covering the nest. Late and excessive melt water saturated one nest with young chicks (they likely died from exposure), and the collapse of one nest built upon snow caused the second case of brood loss. Nine addled eggs were found, and one egg disappeared during incubation in a nest that was ultimately successful. Loss of six nestlings was detected, with disappearance of two chicks from each of two nests occurring at approximately 1 wk and 20 d of age. Only two dead young were observed. One nestling may have starved after falling from the nest. The other nestling apparently succumbed to an infestation of the parasitic fly *Protocalliphora avium* at about 10 d of age (G. Bennett, pers. comm. 1985, and G. Wobeser, pers. comm. 1986).

Pesticide (organochlorine) concentrations from addled eggs collected in 1983 were low (R. Bromley and R. Norstrom, unpubl. data), an expected result as both predator and major prey are generally resident in the Arctic.

#### Post-fledging

Young falcons remained within 200-300 m of the nest for the first 7-10 d post-fledging but by 2 wk travelled up to 1 km away. They would, however, return to the nest area on a regular basis, especially when prey was being supplied by one of the adults. By 20 d post-fledging, young in some territories had moved away from the general vicinity of the nest.

There has been only one band reported to date from the 91 young banded at Kilgavik (95% of known production 1983-86). A juvenile male was captured in mid-September in Cambridge Bay, 145 km northeast of its nest site, approximately 6 wk post-fledging.

## DISCUSSION

### Density and Nest Sites

The density of gyrfalcons breeding at Kilgavik (one pair·125 km<sup>-2</sup>) approaches the highest known in the world. Regional densities are generally much lower (Cade, 1982). Mid-summer densities across the mid-arctic latitudes of the N.W.T. ranged from one pair·233 km<sup>-2</sup> to one pair·1456 km<sup>-2</sup> (Bromley, 1983; Bromley and McLean, 1986). In northeastern Iceland, reportedly the area with the highest regional population density (Cade, 1982), Nielsen (1986) observed one pair·113 km<sup>-2</sup>. However, in Iceland an average of only 22 pairs was successful each year (one·236 km<sup>-2</sup>), compared to 9.5 pairs at Kilgavik (one·210 km<sup>-2</sup>).

A minimum of 45 raven, 41 golden eagle and 100 rough-legged hawk nests are present on the study area. With these and numerous ledges present, it is unlikely that the availability of nest sites is limiting the density of breeding gyrfalcons at Kilgavik. The regularity in spacing of territories observed in most years supports this conclusion. Newton (1979) suggested that raptors may be evenly spaced where nest sites are freely available and that the distance between nest sites is correlated with food supply.

Gyrfalcon use of stick nests built by ravens has been widely reported (e.g., Kishchinskii, 1957; Cade, 1960; Bromley, 1983; Nielsen, 1986). At Kilgavik ravens were present at least as early as mid-winter, possibly year-round, and began nest construction in April. Interspecific interactions were common in spring between gyrfalcons and ravens, probably representing competition for nest sites. Gyrfalcons have been observed taking over nests newly built by ravens in Iceland (Nielsen, 1986) as well as at Kilgavik. At Kilgavik, gyrfalcons and ravens did have some degree of tolerance for one another, successfully fledging young from nests as close as 65 m apart on the same cliff face. In this case encounters were minimized by each species leaving and returning to its nest by opposite directions.

Unlike many gyrfalcon populations (Hagen, 1952; Swartz *et al.*, 1975; Platt, 1977; Langvatn and Moksnes, 1979), nesting gyrfalcons at Kilgavik did not use rough-legged hawk nests. This difference may reflect the fact that the sites used by rough-legged hawks at Kilgavik tended to be on smaller cliff faces and were often easily accessible to predators. Rough-legged hawk sites generally had poor protection from the elements and often were still snow covered at the time gyrfalcons had completed laying. Use of rough-legged hawk nests by gyrfalcons in other areas may be related to narrower nesting requirements by rough-legged hawks (White and Cade, 1971), a paucity of "better" sites with greater protection and less accessibility or less strict nesting requirements of gyrfalcons in regions of less harsh climate.

Barichello (1983) found that fewer young fledged from southerly oriented nests than from those oriented north, similar to the situation at Kilgavik. Apart from the availability of sites, the use and relative nesting success at sites facing a particular direction is influenced by many factors. As pointed out by

Manniche (1910, cited in Jenkins, 1974:29), in regions above the Arctic Circle north-facing sites would receive solar radiation and heat during the coolest period of the day and avoid receiving direct sunlight during the heat of the afternoon. Signs of overheating by nestlings were observed at west-facing sites during periods of sunshine and little wind. The direction of strong prevailing winds and resultant accumulations of snow must also be a factor.

#### Winter Occupancy

In agreement with other studies (Platt, 1977; Nielsen, 1986), only adult gyrfalcons were observed at Kilgavik in late winter. More males than females were observed in late winter, possibly because males are more involved in territorial establishment and defense (Platt, 1977) and therefore return earlier.

Few data exist on winter occupancy of nesting territories by gyrfalcons (Platt, 1977; Nielsen, 1986). Winter occupancy imparts an advantage in ownership of a nesting territory (Nielsen, 1986) but depends upon a reliable prey base during a time when prey is often scarce and light levels sufficient for hunting are of short duration. Resident arctic hare (*Lepus arcticus*), rock ptarmigan (*Lagopus mutus*) and microtine rodents could provide an adequate winter prey base at Kilgavik (Poole and Boag, 1988). As the study area is located above the Arctic Circle, light intensity and duration around the winter solstice may restrict hunting opportunity and prohibit residency in the dead of winter.

#### The Breeding Season

Participation by males in brooding varied widely among sites, but averaged 13% overall. Other workers reported brooding by males at 1% (Bente, 1981) and 6% (Jenkins, 1974). As the male provides most or all of the food to the female and nestlings for at least the first 10 d post-hatch (Cade, 1982; Poole and Boag, 1988), the differences observed among regions may relate to the degree of food-stress. Under periods of food-stress the male may have to spend most of his time hunting, with little or no opportunity to brood. However, the consistency in male participation in brooding in one pair observed at Kilgavik in 2 yr of different numbers of nestlings and availability of prey (Poole and Boag, 1988) suggested that brooding responsibilities may be generally preset between members of a given pair.

Most late brooding was observed in 1985, when cool, wet weather persisted throughout the mid-nesting period. Although Cade (1960, 1982) and Platt (1977) stated that brooding in gyrfalcons ceased when the young were about 10 d old, other studies have documented brooding up to 19 d (Jenkins, 1978) and 27 d of age (Bente, 1981). No significant relationship was found at Kilgavik on a within-year basis between brooding and weather variables. The tendency for gyrfalcon sites to have a complete overhang and good protection from the elements may mitigate the impact of inclement weather on nestling thermoregulation.

The reduction from number of eggs produced to number of young fledged is difficult to obtain, because of the difficulty in detecting total clutch or brood losses. The reduction estimated for Kilgavik (48%) was higher than the 36% (our calculation) estimated from Icelandic data (Nielsen, 1986). We calculated a "loss" of 38% from mean clutch and brood sizes for Alaskan gyrfalcons reported by Cade (1960); however, this underesti-

mates the true loss by not accounting for sites experiencing total reproductive failure.

Kishchinskii (1957) believed that parasites are partly responsible for gyrfalcons using alternative nests to enable cleansing of heavily infested sites. The observation that *Protocalliphora avium* larval infestation was probably the proximate cause of death of a nestling lends support to this claim. Infestations by dipterous larvae were observed at several sites and were often present or heaviest on the youngest member of the brood. Varying degrees of infestation with fleas (*Ceratophyllus vagabundus vagabundus*, R. Lewis, pers. comm. 1985) were also observed at nest sites occupied by gyrfalcons, golden eagles and rough-legged hawks.

Loss of a brood in 1986 through nest collapse was noteworthy, because the stick nest had been built by ravens that spring but usurped by the gyrfalcon pair before laying. The nest, however, was built on a snow ledge rather than a rock ledge. When the snow melted, the nest fell, killing the 10-d-old nestlings. One other nest built by ravens on a snow ledge in 1986 collapsed with melt; these ravens renested 100 m away. To our knowledge there are no reports in the literature of freshly built raven nests collapsing in this manner early in the breeding season of their construction. Both Roseneau (1972) and Platt (1977) reported loss of 6% of their sites through deterioration with age. Cade (1960) also reported collapse of two stick nests with young gyrfalcons, but the young survived in both cases.

There was no significant difference in productivity between territories used regularly or irregularly. This suggests that the contribution of irregularly used territories was diminished not by reduced breeding success, but by reduced occupancy, such that irregularly used territories may have been occupied only in "good" years. The reasons why some territories and not others were occupied every year possibly relates to both the physical characteristics of the site and nearness to a good prey base. We assumed that each year surplus birds were present that could occupy vacant territories when conditions were amenable. However, on only three occasions did we see gyrfalcons not associated with known nest sites.

#### Influence of Spring Weather on Productivity

The influence of spring weather on breeding success observed at Kilgavik has been noted previously for raptors (Cavé, 1968; Newton, 1979; Newton and Marquiss, 1986), including gyrfalcons (Swartz *et al.*, 1975; Bromley and McLean, 1986; Nielsen, 1986). At Kilgavik, precipitation, in particular, appeared to affect production of young. Spring weather may influence breeding success of raptors both directly and indirectly. Direct effects occur as cold temperatures and high precipitation increase the energy needs of the female (Cavé, 1968) and result in reduced hunting efficiency, and thus feeding rate (Cavé, 1968) and loss of body weight. Since body weight must be high for laying to commence (Newton, 1979; Newton *et al.*, 1983), poor condition of the female leads to delayed nest initiation, and possibly the production of eggs of lower quality and hence lower fledging success (Hochachka, 1985).

Indirectly, spring weather may influence breeding success of gyrfalcons by affecting availability of the migratory and resident prey base (Bromley and McLean, 1986; Poole and Boag, 1988). At Kilgavik, poor spring weather may have retarded the migration of rock ptarmigan into the region, delaying increases in prey availability. In a species that initiates laying and incuba-

tion during or after the arrival of large numbers of its main prey, short periods of poor spring weather may be sufficient to tip the energy balance toward a lowered reproductive season.

The climate at Kilgavik is more severe than that found in most other areas where intensive studies on gyrfalcons have been conducted, possibly contributing to later laying, more specific nesting requirements (e.g., no use of exposed rough-legged hawk nests) and brooding late into the nestling period. Despite the harsh climate, the relatively rich prey base seasonally available (Poole and Boag, 1988) encourages a dense, productive population of gyrfalcons in which the males are able to participate in more than just food provision.

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