

THE OVERWHELMING INFLUENCE OF PTARMIGAN ABUNDANCE ON GYRFALCON REPRODUCTIVE SUCCESS IN THE CENTRAL YUKON, CANADA

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ABSTRACT.—Companion studies of Willow Ptarmigan (*Lagopus lagopus*) and Gyrfalcons (*Falco rusticolus*) in the central Yukon from 1978 to 1983 allowed us to examine Gyrfalcon reproductive performance at 14 nest sites in relation to ptarmigan abundance and other potential effects, including weather variables, the previous year's success, nest site characteristics, and Golden Eagle (*Aquila chrysaetos*) nesting density. Ptarmigan abundance declined six-fold and was mirrored by a significant decline in Gyrfalcon breeding success (breeding failure 58%, clutch desertion 33%). Clutch size showed little variation, although deserted nests held fewer eggs than did successful nests, and there were more four-egg clutches when ptarmigan were most abundant. An average of 2.26 young fledged per nest during abundant ptarmigan years, and 0.18 when ptarmigan were declining. No other factors were correlated with Gyrfalcon reproductive success. Juvenile ptarmigan density had a compensatory effect: even when ptarmigan breeding numbers dipped, Gyrfalcons bred successfully if the proportion of juvenile ptarmigan was high. Clutch initiation date was a good predictor of Gyrfalcon breeding performance. Early clutches had more eggs (67% with 4 eggs compared to 27% in late nests), were less likely to be deserted (5% vs. 59%), and fledged more young (93% vs. 38%). Two Gyrfalcon pairs, supplemented with food in a poor ptarmigan year, fledged young at a rate and schedule comparable to pairs during a peak ptarmigan year. We discuss interesting observations about Gyrfalcon brood success, as well as Golden Eagle nesting density as a potentially important aspect of the reproductive ecology of Gyrfalcons in this population. *Received 12 January 2011, accepted 9 May 2011.*

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MANY STUDIES HAVE FOUND a strong link between reproductive performance in birds and food supply (see Arcese and Smith 1988). Newton (1979) reviewed numerous studies of raptors and concluded that, when nest sites

were not limiting, variation in reproductive success of raptors is largely associated with variations in food supply. He argued that insufficient food leads to loss of weight, incomplete gonad development, insufficient

energy acquisition to lay eggs or attend clutches, and consequently to delayed laying or failure to lay at all.

Gyrfalcons (*Falco rusticolus*) nest early in a climatically harsh northern environment. Limited prey species, an irregular food supply, snow, and severe temperatures are common features at the onset of laying, imposing constraints on Gyrfalcons energy budgets and hunting efficiency, and consequently on body condition and reproductive success. Over most of the Gyrfalcons range, Rock Ptarmigan (*Lagopus muta*) and Willow Ptarmigan (*L. lagopus*) are the major, if not the only available food items (see Nielsen 1986), and both species experience dramatic and cyclic population changes (e.g., Bengtson 1971, Weeden and Theberge 1972, Watson and Moss 1979, Myrberget 1984, Pedersen 1984, Bergerud et al. 1985, Williams 1985, Andreev 1988a). Many studies have inferred a numerical response in Gyrfalcons to changes in ptarmigan numbers (e.g., Cade 1960, Roseneau 1972, Platt 1977, Langvatn and Moksnes 1979, Mossop and Ward 1985), however, few have rigorously explored Gyrfalcons-ptarmigan relations.

We suspect that this simple, cyclic food base is the driving feature regulating reproduction in inland Gyrfalcons populations, and perhaps limiting population size. We utilized this natural phenomenon of a cyclic food supply, to determine if changes in ptarmigan abundance would influence changes in reproductive performance, and we supplemented food to Gyrfalcons when ptarmigan were relatively scarce to see if we could reinforce the correlation between food and reproductive success. We evaluated weather and nest site characteristics, including nest quality and Gyrfalcons reproductive success in the previous year, as well as Golden Eagle (*Aquila chrysaetos*) nesting density, concurrently with ptarmigan abundance to extract potentially confounding influences. Our results corroborate those of Nielsen (1999), but with some important differences.

STUDY AREA

The study area (5,000 km²) lies within the Ogilvie Mountains in the central Yukon. The area is a mosaic of three broad habitat types—upland tundra, flanked by rugged, alpine meadows to the south, and hilly discontinuous, sub-arctic taiga forest to the north. The southern mountains can be characterized as lush alpine communities and a well-developed shrub zone, whereas, in the northern mountains, dry alpine tundra with extensive talus and a poorly developed shrub zone are predominant.

The distribution of vegetation appears largely influenced by drainage patterns which are controlled partly by parent material, but to a much larger extent by permafrost (Ricker 1968). The predominant plant association is a tussock-heath type occurring on a variety of topographic situations. Willow shrub is the predominant riparian vegetation and is widespread.

The mammalian and avian fauna is seasonally variable. Frisch (1982) recorded 127 bird species from the study area; 22 were known to over-winter, of which eight were predatory. Willow and Rock Ptarmigan appeared to be the most common avian winter residents. Thirty-six mammals have been recorded in the area (Youngman 1975), although most of the small mammals remain relatively inactive during the winter, or hibernate.

METHODS

Gyrfalcons Reproduction.—Gyrfalcons nest sites, and therefore breeding pairs, were located during intensive helicopter surveys conducted from February to August during 1977 to 1978 (Mossop et al. 1977, Nelson 1978). Two peripheral sites located in 1980 were added to the census. It was assumed that all Gyrfalcons breeding sites were located within the study area, based on the intensity of the search and the very regular distribution of

nests found. We defined the 'nest' as a specific nesting platform, and a 'site' as the general locality of the nest. Typically the site was a set of outcrops with numerous perches, including feeding perches, and protected winter perches.

A site was considered occupied if adults defended the area or if there were indications of recurring visits by Gyrfalcons, such as fresh guano stains and recent prey remains. Courtship observations in a companion study indicated intense loyalty to the nesting site, irrespective of breeding success (Barichello 2011).

The presence or absence of eggs, and the clutch size, was determined from helicopter searches in early May. Based on repeated visits to some sites, and general knowledge about Gyrfalcons, we assumed that egg laying would be complete by 1 May, and clutch abandonment or loss of eggs would occur after the first week of May.

Laying date was the date when a clutch was initiated and this was known on a few occasions from direct observation. Where dates were unknown, they were estimated by back-dating from either known hatching or fledging dates or from the estimated age of the brood. The reliability of back-dating known hatching and fledging dates has been verified by observations largely from captive breeding facilities (D. Nowlan, pers. comm., Platt 1977), and supported by field studies, including this study. Very little variance in the incubation period, the brood period, or the interval between egg laying has been detected (Nielsen 1986, Poole 1987). For some of the analysis we lumped clutch initiation dates into laying date classes: 1=before 10 April, 2=10–24 April, and 3=after 24 April. Nests were checked periodically, and in particular, close to the predicted fledging dates. These late-brood surveys provided a measure of the number of young fledged and the sex ratio.

Supplemental feeding was initiated in March 1982, a year when ptarmigan were at low den-

sities. Ptarmigan were shot and delivered to known Gyrfalcon feeding perches at four nest sites. Daily supplemental feeding continued at the sites of two pairs that took the carrion until 29 April, well after eggs had been laid.

Ptarmigan Abundance.—An index of ptarmigan abundance was determined by counting territorial males during late April on a 4-km² plot within the study area, aided by a bird-dog and replicated at least twice within a 3-day period. It was assumed that all territorial males were counted within the sampling area. This measure of territorial male density was assumed to provide a reliable indication of abundance and population trend of ptarmigan in the Gyrfalcon study area. If territorial male ptarmigan density was less than 10/km², ptarmigan abundance was considered low, and if over 20/km², ptarmigan abundance was considered high. An index of young ptarmigan was derived by multiplying the number of ptarmigan breeding pairs by the proportion of the previous year's chicks in a late winter sample of ptarmigan within the study area.

Weather.—As nearly all egg-laying occurred in April, at a time when the climate was typically harsh and variable, we assumed that the influence of weather on reproductive performance would have its strongest influence in that month. Temperature and snowfall were determined twice daily during the month of April at a Yukon Government highway maintenance camp on the periphery of the study area. Snow accumulation, measured at the beginning of April, was determined by the Water Resources Branch of Canada's Department of Environment at a regularly checked site in the middle of the study area (Petersen 1985). Three weather measurements were used in the analysis: the number of April days where temperatures dropped to -30° C or colder, the number of April days when snow fell, and the snow accumulation in early April. Weather data were pooled into three cold classes (1=11%–30% cold-days, 2=31%–50% cold-days and 3=51%–70% cold-days); two snowfall classes

(1=10%–20% snow-days, 2=21%–30% snow-days); and two snow depth classes (1=<55 cm, 2=>55 cm).

Nest Characteristics.—Earlier analysis (1978–1982) from the study population (Barichello 1983) had related habitat and a number of nest site attributes—elevation, orientation, cliff height, type of nest (stick or ledge), the degree of overhang over the nest, and the presence of sidewalls at the nest—to the current year’s reproductive performance. An index of nest protection, which incorporated both the degree of overhang and the angle of exposure, was the only measure found to be associated, albeit weakly, with eventual Gyr Falcon reproductive success. The index of protection (PI), was deemed to be the only measure of the nest that may influence Gyr Falcon reproductive success, and so was included in this 6-year analysis, treated by PI class (>60 and <60).

Previous Year’s Success.—Productivity in one year was tested against the success of the nest in the previous year. If young had been fledged from a nest in the previous breeding season, the nest was considered to be previously successful, otherwise it was considered unsuccessful.

Golden Eagles.—Golden Eagle nesting density and brood size was determined concurrent with helicopter searches of Gyr Falcon nests in the study area from 1978 to 1982. Forty-one eagle nesting sites were checked per year, and brood size was recorded among those that were active. Comparisons were made between Golden Eagle production and Gyr Falcon fledging success (those eggs that successfully hatched and yielded young that fledged).

RESULTS

Overall Breeding Performance of Gyr Falcons.—Eleven to 14 nest sites within the study area were visited from 1978 to 1983. Pooling the data from different years yielded reproductive data on 77 cases. Sites were occupied

across years 87% of the time. Eggs were laid in 73%, and young were fledged in 53% of the nests observed (Table 1). Three- and four-egg clutches were most common; of 47 clutches of known size, 94% held 3 or 4 eggs (average = 3.3 eggs). The average number of young fledged was 1.5 per nest checked, and 2.1 fledglings per clutch.

The primary causes of reproductive failure (36 failures in total) were failure to lay (58% of all failures), and nest desertion (33% of all failures; see Table 1). Of all known egg failures (65 of 156 eggs), 55% were due to desertion, 17% due to brood predation, and 28% to other unknown egg or brood failures. With the exception of brood predation, all recorded losses of young occurred within the first few days after hatching.

Deserted nests had smaller clutches (2.9 eggs/clutch; $n = 12$) and were laid later (mean laying date=30 April) than nests where eggs were hatched (3.4 eggs/clutch; $n = 44$; $p < 0.01$; Mann-Whitney-U-test; and, mean laying date=12 April; $p < 0.01$; U-test). Nests which successfully hatched and fledged only a portion of the eggs laid ($n = 19$) had similar clutch sizes and laying dates to those nests where all known eggs yielded fledged young ($n = 15$; $p = 0.89$; U-test; and $p = 0.08$; U-test; respectively).

Gyr Falcons began laying as early as 24 March, and as late as 6 May, a 44-day range in the date of clutch initiation. The median laying date was 12 April. Over 50% of all clutches were initiated between 4 and 20 April. Clutch initiation date was a good predictor of breeding performance. Early clutches were more successful in producing eggs ($p = 0.03$; Kruskal-Wallis-test) and fledging young ($p < 0.01$; KW-test). For example, 67% of all early clutches had 4 eggs and 93% of all eggs laid in early nests ($n = 21$) fledged young, in comparison to only 27% and 38%, respectively, from late nests (after 24 April; $n = 17$; Table 2). Late nests had a tendency to suffer much higher nest

Table 1. Gyrfalcon nesting success, ptarmigan density, and Golden Eagle production, within the study area from 1978 through 1983.

	Year					
	1978	1979	1980	1981	1982	1983
Gyrfalcons						
No. sites monitored	11	12	14	14	12	14
No. sites occupied (%)	(100)	(92)	(100)	(100)	(75)	(57)
No. sites with eggs (% of Occ)	10	9	14	10	8	6
No. sites deserted (% of eggs)	0	1	2	5	2	3
No. sites hatched (% of eggs)	10	8	12	5	6	3
No. sites successful (% of Occ)	10	8	12	5	5	3
Median laying date	96	107	99	115	117	113
Mean laying date	94.2	109.1	101.9	110.9	114.4	127.8
No. eggs laid known	25-40	25-35	49-50	32-33	24-36	18
No. eggs laid extrapolated	32.5	30	49.5	32.5	25	18
No. eggs hatched	25-40	21-30	39-45	16-22	14-16	9-10
No. eggs hatched extrapolated	32.5	25.5	42	19	15	9.5
Eggs-extrap./site	3.0	2.5	3.5	2.3	2.1	1.3
Eggs-extrap./site with eggs	3.3	3.3	3.5	3.3	3.1	3.0
4:3 egg clutches	2:5	1:4	8:4	3:5	2:5	3:2
Percent of eggs that hatched that yielded young	75.1	82.4	85.7	52.6	93.3	94.7
No. young fledged/site known	22/9	21/12	36/14	10/14	14/12	9/14
Young/site	2.4	1.8	2.6	0.7	1.2	0.6
Young/successful nest	2.8	2.6	3.3	2.5	2.8	3.0
Experimental Pair						
Eggs laid					3, 4	
Young fledged					3, 3	
Laying date					96, 101	
Ptarmigan						
Territorial male density	25	22	30	9	7	5
Prop. Yng ptarmigan late winter	0.50	0.23	0.36	0.27	0.23	0.12
Golden Eagle						
Occupied sites (of 41 checked)	26	19	12	28	14	U
Young produced	41.6	28.5	18.2	38.2	21.6	U

desertion, as indicated above; 59% of late nests were deserted as compared to 5% of earlier nests (prior to 25 April). Overall, the median laying date was strongly correlated with the number of Gyrfalcons fledged ($r = -0.92$).

Ptarmigan and Gyrfalcon Breeding Performance.—On the ptarmigan census plots, densities of territorial male ptarmigan varied from 5 to 30 per km² (Fig. 1). Ptarmigan were abundant from 1978 to 1980 (22–30 males/km²), and relatively scarce in years 1981 to 1983 (5–

9 males/km²). The proportion of ptarmigan that were chicks in the previous year, within the late winter sample, ranged from 0.12 to 0.50 between 1978 and 1983. The projected density of young ptarmigan ranged from 0.60 to 12.50 (territorial males x proportion that were last year's chicks).

Gyrfalcon breeding performance was linked to ptarmigan abundance. Fewer young Gyrfalcons were fledged per nest in ptarmigan-poor years (0.83/nest; $n = 40$ nest visits), as com-

Table 2. Gyrfalcon nesting success by ptarmigan abundance class.

Gyrfalcon reproductive measures	Ptarmigan abundance class	
	Density <10/km ²	Density >10/km ²
No. of sites observed	40	37
No. of sites occupied (% of sites observed)	31 (78)	36 (97)
No. nests in which eggs were laid (% of sites occupied)	23 (74)	33 (92)
No. nests in which at least one egg was hatched (% of nests in which eggs laid)	14 (61)	30 (91)
No. nests in which young were fledged (% of nests in which eggs were hatched)	12 (86)	27 (90)
Mean laying date (+sd)	112.65 (11.61)	101.18 (11.80)
Median laying date (n)	113 (23)	99 (33)
Eggs counted	71	85
Eggs deserted (% of eggs laid)	27 (38)	8 (9)
Other egg/brood losses (% of eggs laid)	14 (20)	16 (19)
Mean clutch size (+sd)	3.23 (0.61)	3.40 (0.58)
Number clutches w. 4-eggs (%)	7 (32)	12 (44)
Mean no. young fledged (+sd)/clutch laid	1.44 (1.50)	2.55 (1.23)
Mean no. young fledged (+sd)/site	0.83 (1.34)	2.26 (1.42)

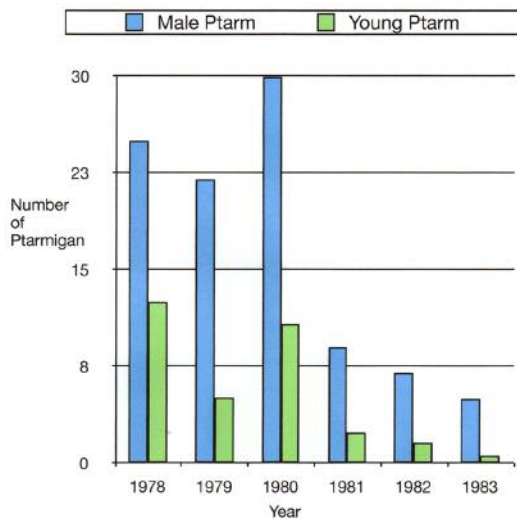


Figure 1. Density (number per km²) of territorial male ptarmigan per year.

pared to ptarmigan-rich years (2.26/nest; n = 37 nest visits; $p < 0.01$; U-test; Table 2). Indeed, 92% of the variation in the average annual Gyrfalcon production could be explained by territorial male ptarmigan density along a linear regression ($y = 4.29 + 1.06(x)$ with $n = 6$; Fig. 2). Although convincing, we were curious about an apparent anomaly. During a year when ptarmigan numbers remained high, there was a drop in the number of Gyrfalcons that were fledged. By comparing the Gyrfalcon production in the 3 years when ptarmigan density was high with the projected number of young ptarmigan in the population (male ptarmigan density \times proportion of young ptarmigan), we found that as expected there was a strong correlation between overall Gyrfalcon production and young ptarmigan density ($r = 0.95$). So, it would appear that the

number of Gyrfalcons fledged is dictated by absolute ptarmigan numbers, but moderated by the proportion of last year's chicks in the population. High ptarmigan densities combined with a high proportion of youngsters appeared to have the greatest influence on Gyrfalcon production ($r^2 = 0.95$).

Not surprisingly, in years when there were fewer ptarmigan, Gyrfalcons initiated their clutches later and laying was spread over more days than when ptarmigan were abundant (see Table 2; $p < 0.01$; U-test). In fact, 85% of the variation in the median laying date could be attributed to the density of ptarmigan ($y = 119.74 - 0.74(x)$; where $n = 6$; Fig. 3). The projected number of young ptarmigan had an even more convincing influence on the median ($r^2 = 0.95$) and the mean laying date ($r^2 = 0.97$).

Gyrfalcon reproductive failures were most evident early in the nesting cycle. In the 3 years when ptarmigan were scarce, there were fewer Gyrfalcon nests in which eggs were laid (62%, as compared to 89%; see Table 2), which was the result of fewer known occupied sites (78% as compared to 97%), and fewer pairs laying (77% vs. 92%). In Figure 4 we show the survival of a potential of 100 eggs (based on a maximum clutch size of 4) across the reproductive period, for years when ptarmigan were abundant and years when ptarmigan were relatively scarce, including the year (1980) when ptarmigan were at their peak.

Mean clutch size varied little between ptarmigan-poor and -rich years ($p = 0.33$; U-test). However, in 1980, when ptarmigan were particularly abundant, there was a higher percentage of four-egg clutches (62%), as compared to other years (20%–40%). Also, successful clutches held an average of 3.5 eggs, whereas the average clutch size from abandoned nests was only 2.9 eggs.

Eggs were less likely to result in fledged young in ptarmigan-poor years; the mean number of young fledged per clutch laid was 1.4 in poor

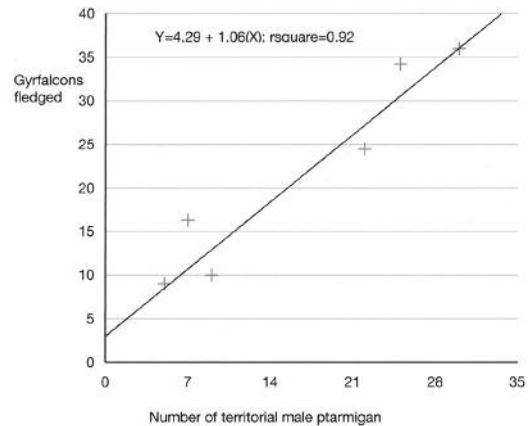


Figure 2. Number of Gyrfalcons fledged in relation to the density of territorial male ptarmigan.

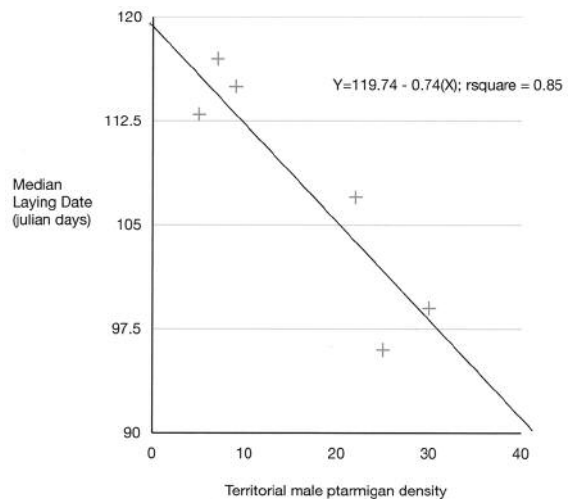


Figure 3. Gyrfalcon median laying data in relation to the density of territorial male ptarmigan.

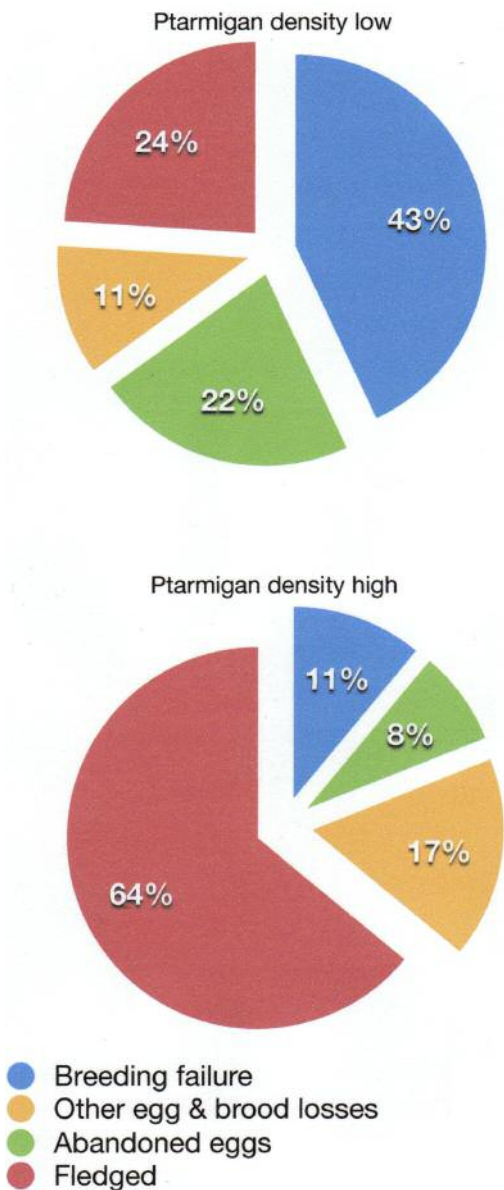


Figure 4. Gyr falcon reproductive attrition (%) during years when ptarmigan were at high density (1978–80) compared to years when ptarmigan were at low density (1981–83). Segments represent losses due to breeding failure, abandoned eggs, and all other egg and brood losses. The red segment represents the percentage of all potential eggs that resulted in fledged young.

years, and 2.6 in good years ($p=0.01$; U-test). Clutch desertion was much more common in poor years – 38% of all clutches laid (representing 33% of all eggs laid) were deserted, as compared to only 9% of all clutches laid in the good ptarmigan years. Partial losses of the clutch or brood from nests that successfully fledged at least one young were unrelated to ptarmigan abundance classes (20% and 19% of eggs failed from successful nests in poor and good ptarmigan years; see Table 2).

Ptarmigan abundance, then, was a major factor governing Gyr falcon breeding performance, by influencing the number of sites occupied, the number of nests where eggs were laid, the laying date, the number of nest desertions, and consequently the number of young fledged per nest. Most adjustments occurred early in the nesting period, and compounding the losses, 91% of all nest failures were a result of failure to breed or abandoning the clutch. The number of young ptarmigan in the population had an additive effect on Gyr falcon production, with a particularly strong influence on the timing of clutch initiation.

Weather and Breeding Performance.—April weather was variable during the study period. Mean temperatures varied from -6.5 to -10.7° C, and cold-days (those days when temperatures dropped to lows of -30° C or colder) ranged from 8 to 21 days in April. The number of days it snowed in April (4–8 days) was inversely related to the number of cold days ($r = -0.91$; $n = 6$). Snow accumulation in early April varied from 49 to 94 cm. We could find no correlations of any April weather variable (number of cold-days, number of snow-days, or snow accumulation) with any parameter of Gyr falcon breeding performance ($P>0.05$; U-tests, and KW-test).

Habitat, Nest Sites and Previous Breeding Performance.—Reproductive performance between sites was variable. For example, the average number of young fledged per site varied from 0.3 to 2.5. We suspect reproductive

success derives from a number of attributes, including the quality of individual breeders, territory quality, nest quality, or perhaps the previous reproductive success. Adults were unmarked so we had no knowledge of breeding history of pairs or individuals. Based on habitat features, including general topography and broad vegetation characteristics, we could find no connection with any of the reproductive parameters and three different habitats ($p > 0.17$; KW-test).

There appeared to be a subtle influence of nest quality, as defined by an index of nest protection – a measure of overhang combined with side-walls—on reproductive performance (Barichello 1983), although all statistical tests were insignificant ($p > 0.10$; U-test). Poor quality nests ($PI < 60$) were known to be occupied in 79% of cases (22/28), in comparison to higher quality nests ($PI \geq 60$) which were found occupied in 92% of 49 cases ($p = 0.10$). There were fewer occasions of egg-laying from sites with poor quality nests (61%) due to lower occupancy of these sites, as compared to sites with higher quality nests (eggs were laid 80% of the time). Clutch size and the number of young fledged per clutch varied little between PI classes.

Nests that fledged young in the previous breeding season were more apt to be occupied in the current year ($p = 0.04$; U-test). However, no benefits of previous reproductive success were observed on egg laying, laying date, clutch size, number of young fledged per clutch, or overall production ($p > 0.21$; U-tests).

Golden Eagles and Gyrfalcon Brood Success.—The number of Golden Eagles produced varied from 18 to 42 from 41 nest sites checked between 1978 and 1982 within the study area. The proportion of Gyrfalcon eggs that hatched and yielded young ranged from 0.53 to 0.93 during the same period. Although sample sizes were small, it appeared that when Golden Eagle production was high, Gyrfalcon

egg/brood survival (not including deserted clutches) was low ($r = -0.75$, $n = 5$ years).

Feeding Experiment.—In 1982, beginning on 19 March, ptarmigan carcasses were left at four Gyrfalcon sites. At two sites, the resident pairs began to remove the carrion, and supplemental feeding was continued at these two sites for the next 40 days. They were presented with 46 and 49 intact ptarmigan, of which 43 and 46 were removed or eaten, or approximately 94% of the items provided. Observations indicated that males were retrieving the carrion and presenting intact ptarmigan to females. The rates of consumption of the carrion by the pairs was 1.1 and 1.2 ptarmigan per day, rates similar to courtship feeding rates observed during a year of good Gyrfalcon productivity (Barichello 2011).

The experimental pairs produced three and four eggs, and each fledged three young per nest, in a year when eggs were found in only 66% of control nests ($n = 12$), and the average fledged brood size was 1.2 per nest, and 1.6 per occupied nest. Clutch initiation date, as a predictor of reproductive performance, was also advanced in the experimental nests as compared to the control nests. The provisioned Gyrfalcon pairs produced eggs and fledged young at a rate consistent with average production in a year of generally high productivity. Clutch initiation dates of experimental pairs were also similar to laying dates observed in the year when Gyrfalcon productivity was highest (1980).

DISCUSSION

Food and Reproductive Success.—Gyrfalcons have long been known to be associated with ptarmigan. The influence of ptarmigan density on Gyrfalcon reproductive performance in this study was overwhelming, and reaffirmed through experimental feeding. These results are consistent with numerous other raptor studies where productivity increased with an increase in prey density, e.g., Kestrels (*Falco*

tinnunculus) (Cave 1968), Sparrowhawks (*Accipiter nisus*) (Newton 1986), Tawny Owls (*Strix aluco*) (Southern 1970, Wendland 1984), Tengmalm's Owl (*Aegolius funereus*) (Korpimäki 1985), Great Horned Owls (*Bubo virginianus*) (McInvailee and Keith 1974), Ferruginous Hawks (*Buteo regalis*) (Smith et al. 1981), and Golden Eagles (Smith and Murphy 1979). Similarly, greater productivity induced by supplemental feeding has been reported for Sparrowhawks (Newton and Marquiss 1981), Kestrels (Dijkstra et al. 1982), Crows (Yom-Tov 1974), Magpies (Hogstedt 1981) and Song Sparrows (*Melospiza melodia*) (Arcese and Smith 1988). In all cases, food appeared to play a significant role in reproductive performance, as emphasized by Lack (1954), Immelmann (1971), Newton (1979), and Drent and Daan (1980).

The number of young (yearling) ptarmigan appeared to have an additive effect on Gyrfalcon production in our study. Gyrfalcon hunting success and therefore courtship performance is likely enhanced when there are many young vulnerable ptarmigan in the population; this should yield higher Gyrfalcon production. It is of interest that, in Nielsen's (1986) Icelandic study, Gyrfalcon laying success was influenced by ptarmigan density but only during the increase phase of the ptarmigan cycle. We suggest that proportionally more juvenile ptarmigan are typically found during the increase phase, and this would improve Gyrfalcon reproductive success.

Other Factors and Reproductive Success.—No other factor was found to influence Gyrfalcon reproductive performance, although the previous year's reproductive success may have influenced the establishment of territorial pairs; that is, Gyrfalcons were more apt to occupy nest sites that had been successful in the previous breeding season. Platt (1977) found Gyrfalcons to be faithful to successful nesting sites and more frequently abandoning unsuccessful sites. Similar findings have been reported, particularly among males, for Spar-

rowhawks (Newton 1986), Peregrines (Ratcliffe 1980; Mearns and Newton 1988), and Tengmalm's Owl (Lofgren et al. 1986; Korpimäki 1988). The common theme is that preferred nesting sites were better, and therefore occupied first, possibly by more experienced pairs, who remained faithful to these sites if they were successful. Why this did not translate into higher productivity at previously successful nests in our study may be a result of so few site vacancies over the study period.

Despite breeding in late winter when snow and severe temperatures were the norm, the perceived quality of the nest, as defined by how well-protected it was, had no significant influence on reproductive success. Gyrfalcons tended to nest in well-protected cavities, or exposed nests on southerly exposures where snow-melt was advanced (Barichello 1983). Gyrfalcons were probably selective in their choices of sites, the effect of which was to reduce the variation in nest quality at active Gyrfalcon sites. We suspect that insufficient variation in nest quality or the overwhelming importance of food overshadowed any effects of nest quality (as measured by protection) on reproductive performance of the study population.

Some Gyrfalcon studies have suggested that weather may influence reproductive success (Swartz et al. 1975, Nielsen 1986, Poole 1987). The severity of temperatures during incubation, the delay of spring, and melt-freeze conditions have been proposed as possible factors. Intuitively, weather could also influence Gyrfalcon reproductive performance through ptarmigan vulnerability. For example, cold weather induces snow-roosting (Andreev 1988b), snow cover could influence the conspicuousness of ptarmigan (Nielsen 1986), and snow accumulation might reduce the availability of escape cover. Additionally, persistent winters and therefore delays in ptarmigan courtship, may reduce Gyrfalcon hunting efficiency, and therefore reproductive success. However, we found no influence of tempera-

tures, snowfall, or snow accumulation on Gyrfalcon reproductive success despite wide variation in climatic conditions. We concur with the views of Newton and Marquiss (1984) in their study of Sparrowhawks, that weather acts indirectly on reproductive performance, by influencing the availability of food. We suspect that weather's greatest influence on Gyrfalcon reproductive success is through its effect on the scheduling of ptarmigan courtship, where delayed ptarmigan courtship will debilitate Gyrfalcon breeding success.

Mechanisms of Regulation of Reproduction.—Although numerous studies have related Gyrfalcon breeding density to changes in ptarmigan abundance (e.g., Dementiev 1960, Bengtson 1971, White and Cade 1971, Gudmundsson 1970, Swartz et al. 1975, Platt 1977, Langvatn and Moksnes 1979, Nielsen 1986, Mossop and Ward 1985), the mechanisms are largely obscure. Nielsen (1986) found that most Gyrfalcon sites were occupied in most years and the frequency of laying tracked ptarmigan density, but only during the increase phase. Swartz et al. (1975) and Roseneau (1972) suggested that Gyrfalcons vacated sites and emigrated to prey-rich areas as a response to ptarmigan declines.

Non-laying and Clutch Desertion.—In our study, most Gyrfalcon nest failures were due to non-laying (58%) and clutch desertion (33%), and both were strongly associated with ptarmigan abundance. Non-laying was a result of site vacancies (28% of all failures), combined with failure of territorial pairs to lay (30%). Newton (1986) similarly found the most common reproductive failures of Sparrowhawks to be non-laying due to reduced territory occupation, breeding failures of territorial pairs, and clutch desertion. Failure to lay eggs is the simplest response to food scarcity and a common response, particularly in northern species or species exploiting a simple, cyclic food supply (Drent and Daan 1980). This relatively immediate response to food scarcity avoids the high

cost of producing a brood when its survival is very uncertain.

We suspect that the failure to breed is a result of failure to gain weight and its associated hormonal changes. Females that are insufficiently fed lose weight and are presumably apathetic toward breeding, and perhaps motivated to hunt, further impairing their ability to gain the weight necessary to manufacture eggs, which can be as much as 15% of body weight.

Clutch desertion occurred most frequently from late nests that typically held fewer eggs, and failure occurred early in the incubation period. This pattern is similar to clutch desertion in Sparrowhawks (Newton 1986). Nest desertion is likely a consequence of a pair unable to provision themselves while attending a clutch.

Laying Date.—Clutch initiation date was a good predictor of eventual Gyrfalcon productivity, and associated with ptarmigan abundance. Supplemental feeding also resulted in advanced laying. These results are consistent with findings from several species (see Arcese and Smith 1988, Daan et al. 1988, Beukeboom et al. 1988). Newton and Marquiss (1984) found that delayed laying in Sparrowhawks was associated with lighter body weights, poorer territories, inexperience, and relative scarcity of prey, and further, that birds that fledged early were more likely recruited into the breeding population. They concluded that the timing of egg-laying is an inherited trait, and delays in laying are a result of compromising conditions, particularly food supply. Likewise, we suspect in Gyrfalcons there is a predisposition to nest early, but to delay if food is insufficient. Also, if young ptarmigan are easier to catch, the number of last year's chicks in the population should influence laying date, as suggested by our findings in the Ogilvie Mountains.

The advantage of early laying to Gyrfalcons is not immediately obvious. Early clutch initia-

tion in the study area coincided with potentially severe weather and low diversity of potential prey. However, Gyrfalcons have a long nesting period relative to the length of the growing season at these latitudes. Much of the northern avian fauna is migratory, and small hibernating mammals become relatively unavailable after a short reproductive period. It may be that the timing of fledging is far more important to Gyrfalcon fitness than the timing of clutch initiation. Young fledged early leave the nest at a time when their prey is most abundant, many of which are young and inexperienced. In particular, it is an opportune time to exploit emerging young and inexperienced Ground Squirrels (*Spermophilus arcticus*). These small hibernating mammals, preoccupied with storing fat, may be an important resource to Gyrfalcons learning to hunt. Fledging at a time when their prey is abundant, active, and untested, may not just be an advantage, but a necessity in enabling young Gyrfalcons to acquire the skills of hunting. Fledged too late, young Gyrfalcons may have difficulty hunting, with consequently low survival, reinforcing the advantage of early laying.

Clutch Size, Egg Failures, and Brood Losses.—There was little natural variation in Gyrfalcon clutch size, and supplemental feeding did not result in more eggs per clutch than observed in control nests. Similarly, Dijkstra et al. (1982), although able to increase the clutch size of European Kestrels with additional food, found no clutch adjustments beyond that predicted from laying date, and Arcese and Smith (1988) could not produce larger Song Sparrow clutches than those observed naturally. Arcese and Smith (1988) hypothesized that clutch size is limited by genetic and developmental factors, rather than the availability of high quality food, except at very high population densities, or in unfavourable years or habitats.

In our study, natural adjustments in clutch size occurred, albeit slightly, only in the very best year (1980). During this year there were proportionally more four-egg clutches than in all

other years. Large raptors rely on the accumulation of body reserves to produce a clutch (Newton 1977). This tendency suggests that large raptors must attain a weight threshold before laying. Drent and Daan (1980) suggested that weight or condition may be a prerequisite for breeding in a number of species, acting as a signal to which females may adjust their reproductive commitment. Such a strategy appears to apply to Gyrfalcons, enabling them to adjust to food stress, largely by refraining from laying until they attain threshold weight. The higher frequency of four-egg clutches during a year ptarmigan were abundant in the Ogilvies, suggests that more females were able to sustain their weight during the period of egg-laying, more so than in an average year, perhaps aided by the proportion of young ptarmigan in the population.

Egg failures other than desertions were relatively insignificant to eventual productivity, and not explained by food (ptarmigan) abundance. Only 12% of all eggs laid in successful nests failed (partial clutch and brood losses), and the loss was relatively consistent between years.

Golden Eagles may have had a subtle effect on Gyrfalcon brood success. Conceivably Gyrfalcons are discouraged from hunting near active Golden Eagle nests due to the threat they impose of predation or kleptoparasitism. The resulting effect would be a functional loss of foraging habitat to Gyrfalcons, consequently longer hunting forays, and therefore longer periods away from their nests. This would put the brood at greater risk to predators, including ravens, gulls, and Golden Eagles. Higher nesting densities of Golden Eagles would exacerbate this potential risk, as suggested by our study.

However, the effects of Golden Eagles on Gyrfalcon production are likely dwarfed by the more substantive effect of ptarmigan abundance early in the nesting period. Perhaps the more serious impact of Golden Eagles is that

they potentially remove (directly or indirectly) young Gyrfalcons which may be important recruits to fill territory vacancies when ptarmigan are again abundant.

Food Supply and Reproduction: Summary.— Gyrfalcon reproduction in the study area appeared largely dictated by ptarmigan abundance, having its greatest influence early in the nesting season. When ptarmigan were scarce, non-laying, delayed nesting, and clutch desertions were common among Gyrfalcons. Minor variation of clutch size, egg viability and brood survival were observed, but these adjustments were largely independent of ptarmigan abundance.

The strong influence of ptarmigan on Gyrfalcon performance supports the arguments of Drent and Daan (1980), Newton (1979, 1980), and Arcese and Smith (1988) that there is a direct and pervasive link between food supply and reproductive performance of birds. We suspect that ptarmigan have not only shaped the evolution of Gyrfalcons, but they are currently an important factor regulating population size, mediated through territorial behavior and reproductive performance.

The difference between Gyrfalcon reproductive success and ptarmigan numbers, as observed in Iceland (Nielsen 1999) and in this study, is puzzling. Nielsen (1999) found that the Gyrfalcon population he studied in Iceland between 1981 and 1997 relied on Rock Ptarmigan as their staple diet in all years. Ptarmigan were the only available supply of food at the onset of nesting. The number of occupied Gyrfalcon sites and the number of sites where young were fledged was not directly tied to ptarmigan numbers, but rather tracked ptarmigan with a 2-year lag. Nielsen (1999:1046) surmised that early laying and the overriding influence of spring weather, and not ptarmigan numbers, affected Gyrfalcon breeding success.

Gyrfalcon reproductive ecology appears to vary across their distribution, for reasons that

are unclear. Comparisons between Gyrfalcon populations in Iceland and the Yukon are particularly difficult to make because of some very distinct differences. Iceland Gyrfalcons rely on Rock Ptarmigan and many reside in coastal areas, whereas central Yukon Gyrfalcons live inland and rely primarily on Willow Ptarmigan. In the central Yukon, ground squirrels are a very important part of the diet, but do not occur in Iceland.

As for reproductive performance, Iceland Gyrfalcons consistently under-performed Yukon Gyrfalcons when ptarmigan numbers were above average. In these years, proportionally fewer Gyrfalcon nesting territories were occupied (71% in Iceland vs. 97% in the Yukon), fewer nesting territories fledged young (34% vs. 73%), and fewer occupied territories fledged young (48% vs. 75%) in Iceland as compared to the Yukon. Much less variation between geographic areas was observed when ptarmigan numbers were below average (63% vs. 78%; 30% vs. 30%, and 48% vs. 39%, respectively).

We propose two factors that may explain why the relationship between Gyrfalcon breeding success and ptarmigan numbers differed in the Yukon and Iceland. First, Gyrfalcon kill rates were higher during low ptarmigan years in Iceland (32% of the adult population removed during low Ptarmigan years, as compared to 11% during the peak) (Nielsen 1999). Such a functional response would, as suggested by Nielsen (1999), dampen the numerical response. It is possible that Rock Ptarmigan become more vulnerable during the decline phase, possibly because of the prevalence of non-breeding flocks. Willow Ptarmigan may be less vulnerable during the decline phase due to their predator avoidance strategy of concentrating in high willow stands. Consequently kill rates of Gyrfalcons in the Yukon may at best remain stable, but possibly decrease as ptarmigan decline. It may be noteworthy that in Sweden, Nystrom et al. (2006) found Rock Ptarmigan in the Gyrfalcon diet in greater pro-

portion to their estimated population size than Willow Ptarmigan, suggesting that they are more vulnerable to Gyrfalcon predation.

Second, there may be poorer levels of Gyrfalcon recruitment in Iceland due to the absence of ground squirrels. Ground squirrels are possibly a critical component of the Gyrfalcon summer/fall diet, particularly at the time of fledging. This may benefit Gyrfalcon survival and be most crucial when ptarmigan are at low densities. Perhaps very low Gyrfalcon survival rates in Iceland during ptarmigan lows reduce the number of available recruits at a time when ptarmigan are abundant, and therefore dampens the opportunity to increase production.

Inadequate recruitment when ptarmigan were low in numbers, which may have limited the number of Gyrfalcon breeding pairs when ptarmigan were high, combined with higher rates of predation when ptarmigan were declining, may explain why Iceland Gyrfalcons did not immediately respond to numerical changes in ptarmigan, as was evident in this study.

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