GYRFALCON COURTSHIP—A MECHANISM TO ADJUST REPRODUCTIVE EFFORT TO THE AVAILABILITY OF PTARMIGAN

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ABSTRACT.—I watched six pairs of Gyrfalcons (*Falco rusticolus*) in the central Yukon during the courtship period and recorded six courtship behaviors during 385 h of observation in 1980 when ptarmigan were abundant, and 465 h in 1981 when they were scarce, to determine if courtship provided the mechanism by which Gyrfalcon pairs adjust reproductive effort to ptarmigan numbers. It appeared that courtship feeding was the principal cue, presumably through weight gain, to entice the female to the nest and invoke breeding. Courtship feeding dropped significantly from one year to the next, and was associated with the decline in the number of ptarmigan (one delivery per 27.5 h in 1980 versus one per 58.1 h in 1981), and was consistently higher from successful sites and those where laying was advanced. The reduced frequency of food delivery was associated with female apathy – less loyalty to the site and indifference to the nest. This prompted greater frequency of male courtship displays. These activities – nest visits, copulations, and aerial aerobatic displays – were more frequent and extended into the post-laying period when ptarmigan were scarce (1981), and were more evident of failed and delayed nests. The likely function of such behavior was to seduce passive females. Intense male displays, however, appeared to be no substitute for food provisioning, as eventual failures were common where advertising was frequent and provisioning rates were low. The male did not appear to compensate by hunting more when ptarmigan were scarce – his presence at the site varied little between years. It is likely that the risk of losing his territory was much higher when he was absent, with obvious long-term implications. Courtship feeding likely serves three principal functions – it allows the pair to refrain from the high cost of reproduction when success is unlikely, it provides criteria on which the female can discriminate among males and nesting territories, and it strengthens the pair bond and so enhances future breeding efforts. Aborting the reproductive effort early when failure is likely may improve the ability of pairs to over-winter and retain nesting territories, and so contribute to long-term reproductive success. *Received 17 January 2011, accepted 20 June 2011*.

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Key words: Arctic, behavior, courtship, Gyrfalcon, prey abundance, ptarmigan, reproductive rate.

In a companion study in the Ogilvie Mountains, Yukon, Gyrfalcon (*Falco rusticolus*) reproductive success was influenced primarily by ptarmigan abundance, having its greatest effect early in the nesting season (Barichello and Mossop 2011). When ptarmigan were relatively scarce, non-laying, delayed nesting, and clutch desertions were common. These observations were consistent with those of other studies (see Nielsen 1999).

If Gyrfalcon reproductive outcomes can be anticipated early in the nesting cycle, what role does courtship play in mediating the adjustments between ptarmigan abundance and the Gyrfalcon's motivation to lay eggs and incubate them? There may be a severe penalty for nesting when success is unlikely, given the high cost of producing young Gyrfalcons due to a lengthy nesting period in these simple and climatically harsh environments, and where nesting territories are likely a limiting factor. Indeed, the ability of adults to over-winter, retain a nesting territory, or survive may be affected. Courtship may thus be instrumental in providing the cues for adult Gyrfalcons to assess their chances of success, and cut their losses when the odds are poor. Presumably this enhances their lifetime reproductive success. Courtship may also provide an ideal mechanism to evaluate mates and/or the quality of the nesting territory. This may be particularly important to the female, whose success is almost entirely dependent on her mate. The purpose of this study was to understand the link between Gyrfalcon courtship behavior and reproductive performance.

Study Area

The study area (5,000 km^2) lies within the Ogilvie Mountains in the central Yukon just north of the 64th parallel of latitude, and is bisected by the Dempster Highway. The area is wet, upland tundra, flanked by rugged, alpine meadows to the south and a hilly, discontinuous, sub-arctic taiga forest to the north. The southern mountains are characterized by having lush alpine communities and a well-developed shrub zone, while in the northern mountains, dry alpine tundra with extensive talus and a poorly developed shrub zone is predominant. The typical plant association is a tussock-heath type occurring on a variety of topographic situations. Willow shrub is the predominant riparian vegetation and is widespread.

Methods

Courtship observations were made from vantage points or permanently positioned plywood blinds at six individual Gyrfalcon nest sites in the Ogilvie Mountains from 18 March to 28 April, in 1980 and 1981. The daily observation period averaged 9.1 h, with most observations falling between 1000 and 1800 hours.

Both sexes were observed concurrently when they were together at the site. A total of 29 activities were recorded; however, I considered six to be specific to courtship, as follows:

1. Fidelity to the site—the amount of time each adult spent at the nest site;
2. Food deliveries by the male to the female;
3. Attention to the nest site—frequency of nest visits, and duration of time on the nest;
4. Copulations;
5. Aerial aerobatics, and;
6. Mutual encounters.

Behaviors were recorded in minutes and coded as either instantaneous or continuous. Continuous activities were recorded with initiation and termination times. Frequency and duration were determined for these activities. Brief or instantaneous activities, such as copulations, were recorded with only an initiation time.

The frequency of courtship feeding was expressed as the average interval between occurrences (observation period/number of food deliveries) or the cumulative frequency of food deliveries against the cumulative hours of observation. Similarly, mutual ledge encounters were recorded in relation to the observation period. All other instantaneous events were presented as an average interval between occurrences, or the cumulative frequency of occurrences, for the time that the adult (whose behavior was recorded) was present at the site. Sustained activities were presented as a percentage of the observation time. Comparisons of percentages which extended over a wide range were made by first transforming the percentages using angular transformations (Sokal and Rolf 1981).

Sexes were identified by size, wing-beat, and plumage. Females are significantly larger than males and had a deeper wing-beat. Females also tend to be more heavily streaked on the breast, and were often darker on the back (Poole 1987, D. Nolan, pers comm.). Once plumages were described for a particular pair, these descriptions were used to help identify and sex birds on subsequent visits. Birds could often be distinguished by the degree of streaking or barring on the breast, the contrast of back and underside, the prominence and shape of the malar stripe, and the size and shape of the white patch at the back of the head. These characteristics varied between birds. Gyrfalcon intruders to the site were sexed and classified by age. Juvenile birds had grey-blue feet and ceres, and appeared more heavily streaked; adults had yellow feet and ceres, with less streaking (Mattox 1969, D. Nolan pers. comm.).

For the analysis, I pooled observations into broad categories—year, laying period (prelaying, laying and post-laying), Gyrfalcon productivity classes (failed to lay, clutch abandoned, successful), and laying date class (prior to 10 April, 10–20 April, after 20 April). I examined the sequence of courtship events in relation to weekly periods, and 5-day periods prior to, during, and after laying. Laying an entire clutch of eggs generally occurs over a 5–10 day period for Gyrfalcons (Platt 1977). Therefore, I considered the period of laying to represent at least five days, beginning with the initiation of the clutch. The pooling of observations into broad categories prevented the calculation of statistical error but was thought to provide a general interpretation of courtship behavior.

RESULTS

Courtship observations took place in 1980 when ptarmigan were abundant, and in 1981 when ptarmigan were relatively scarce (see Barichello and Mossop 2011). A total of 850.6 h of observation were made; 384.5 and 465.1 h in 1980 and 1981, respectively. Observations from six sites varied from 28.6 to 152.3 h per year. Most (77%) observations were recorded from three sites, and most fell between 1000 and 1700 hours. The observation period, with respect to laying phenology and calendar week, was similar in 1980 and 1981 (Figure 1a and 1b). Note that conditions were not ideal to acquire behavioral data. Those nest sites that provided a vantage point from which to view the entire set of cliffs straddled a 100-km stretch of the Dempster Highway, and were up to 15 km off the road. Despite the difficultly of visiting many of these locations, I chose to watch six nesting sites in an attempt to observe courtship activity at sites with different reproductive schedules and outcomes.

Site Fidelity.—The male Gyrfalcons devoted similar amounts of time to the nest site in 1980 (53%) and 1981 (49%). It was only in the post-laying period (for those pairs that laid eggs) that differences in male site fidelity were apparent. In this period in 1980, the male was present at the site 67% of the observation time, compared to only 43% in 1981 (Table 1).

Differences in site fidelity were far more pronounced for the female. She was at the site 85% of the time in 1980, compared to 34% of the time in 1981. Females that laid eggs were equally disloyal to the site (36%) as those that abstained from laying (34%) in 1981. For those females that laid eggs, year-to-year differences in site loyalty were apparent across all

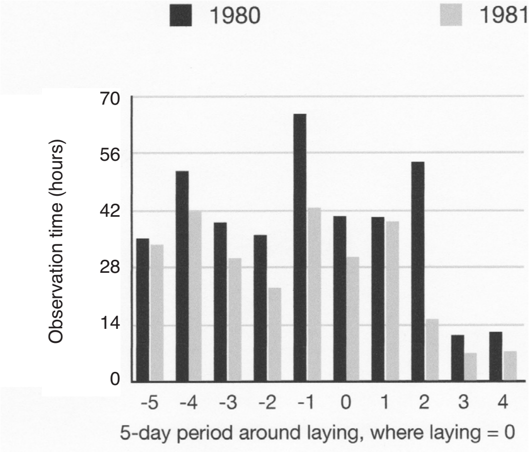

Figure 1a. Hours of observation in 5-day periods around laying in 1980 and 1981.

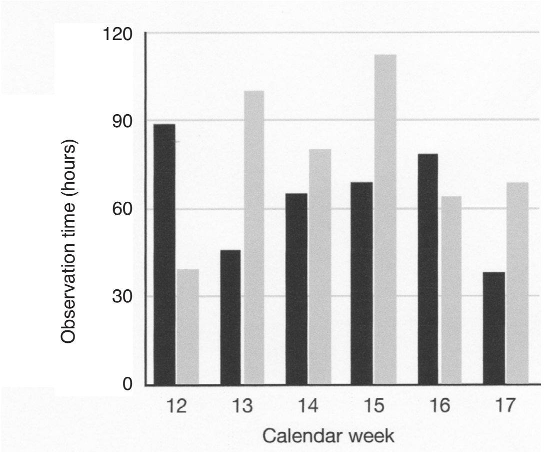

Figure 1b. Hours of observation by calendar week in 1980 and 1981.

Table 1. Gyrfalcon courtship activities (continuous behaviors) in relation to nesting phenology, in 1980 and 1981 (see methods).

Per.	Observation		Male site fidelity				Female site fidelity				Female nest fidelity			
	1980	1981	1980		1981		1980		1981		1980		1981	
	h	h	h	%	h	%	h	%	h	%	h	%	h	%
-5	35.2	33.7	3.7	10.6	9.6	28.6	31.2	88.8	15.1	45.0	0	0	0.0	0.1
-4	51.7	41.7	8.2	15.9	11.2	26.7	30.4	58.9	18.3	43.7	0.1	0.3	0.1	0.3
-3	39.1	30.3	14.8	37.9	19.4	63.7	27.7	70.8	12.2	40.2	0.0	0.1	0	0
-2	36.0	23.0	23.9	66.4	7.1	31.0	24.9	69.2	20.3	88.0	1.4	5.7	7.4	36.7
-1	65.6	42.6	41.5	63.3	30.4	71.4	60.3	91.9	15.6	36.3	21.9	36.4	3.2	20.7
0	40.5	30.6	31.8	78.6	21.0	68.7	40.1	98.9	30.6	100.0	26.5	66.1	20.0	65.3
1	40.3	39.3	25.3	62.9	13.2	33.6	34.9	86.6	36.7	93.4	32.7	93.7	15.3	41.8
2	53.8	15.3	39.0	72.6	8.2	53.2	53.8	100.0	15.3	100.0	38.3	71.1	6.2	40.6
3	11.3	6.9	8.7	77.3	1.0	14.7	11.3	100.0	6.9	100.0	10.5	93.1	6.9	99.6
4	12.1	7.4	5.5	45.5	7.4	100.0	12.1	100.0	7.4	100.0	11.8	97.3	5.9	79.5
Pre	227.6	171.3	92.2	40.5	77.8	45.4	174.6	76.7	10.7	22.6	26.4	15.1	10.7	22.6
Lay	40.5	30.6	31.8	78.6	21.0	68.7	40.1	98.9	20.0	65.3	26.5	66.1	20.0	65.3
Pst	117.4	68.9	78.6	66.9	29.8	43.2	112.0	95.4	34.3	51.8	93.2	83.2	34.3	51.8
TL	385.5	270.8	202.6	52.6	128.6	47.5	326.6	84.7	65.0	36.5	146.0	44.7	65.0	36.5
NL		194.3			99.7	51.3			40.6	30.4			40.6	30.4
Tot	385.5	465.1	202.6	52.6	228.3	49.1	326.6	84.7	105.7	33.9	146.0	44.7	105.7	33.9

Per. = 5-day period around laying where 0 = laying
Pre = Pre-Laying period
Lay = Laying period
Pst = Post-Laying period
TL = Total of those pairs that laid eggs
NL = Total of those pairs that failed to lay eggs
Tot = Total of all pairs observed

Table 2. Courtship activities in relation to year (frequency) and productivity class (average interval in hours between occurrences). Note that the interval between male food deliveries and copulations was relative to the entire observation period, and the interval between nest visits and aerobatic flights was determined only in relation to the time when the male was at the site. Female nest fidelity was the percent of the time she was on the nest while at the site.

	Year		Reproductive Success		
Courtship Activity	**1980**	**1981**	**Productive**	**Abandoned**	**Failed**
Male nest visits	48	78	5.3	3.2	2.8
Female nest visits	50	61	7.2	5.7	4.6
Male aerobatic flights	31	53	10.7	10.1	5.1
Female aerobatic flights	15	41	19.6	12.7	9.3
Food deliveries	14	8	29.4	34.5	48.6
Copulations	21	55	39.2	6.4	3.8
Female nest fidelity (%)	48	39	78.5	35.3	30.0

Productive = sites with nests that eventually fledged young
Abandoned = sites where a clutch was laid but later abandoned
Failed = sites where the pair failed to lay eggs

nesting periods: in 1980 she was present 77%, 99%, and 95% of the time during the pre-laying, laying and post-laying periods, compared to only 23%, 65%, and 52% in the corresponding periods in 1981.

In 1981, it appeared that female site fidelity was a lag response to male site fidelity in the prior period (r^2=0.95). That is, a decline in male presence at the site was followed by a decline in female site fidelity in the following 5-day period (Figure 2). A lag response in female site fidelity to male fidelity in the previous five days was not obvious in 1980.

Altogether, the male stayed home more at sites that yielded young (69% of the time), than those where the eggs were eventually abandoned (48%), or those where the female abstained from laying (51%). Differences in site fidelity were also apparent across laying date classes, for both sexes. From early to delayed clutch initiation classes across years, males were present 68, 52, and 43% of the observation time, while females were present 93, 83, and 60% of the time.

Courtship Feeding.—During the two years of courtship study, food deliveries to the nest occurred on average every 38.7 h of observation. There were substantially more food deliveries in 1980 (14 food drops per 385 h of observation) as compared to 1981 (8 per 465 h). Fewer food drops in 1981 were apparent across the sampling period (Figure 3). Even discounting the pairs that failed to lay eggs, there were more food drops in 1980 in both the pre- and post-laying periods. In the pre-laying period alone, a food drop was made on average every 25.3 h, as compared to every 57.1 h in 1981. Also, in 1981, skirmishes between the male and female (tugs-of-war) over food brought to the site by the male were observed six times. No such food fights were observed in 1980.

Productive and advanced nests enjoyed more frequent food drops. Food deliveries occurred every 29.4 h at sites fledging young, every 34.5 h at sites where eggs were abandoned, and every 48.6 h at sites failing to lay eggs (Table 2). From early to delayed laying classes, food provisioning occurred every 23.8, 28.4

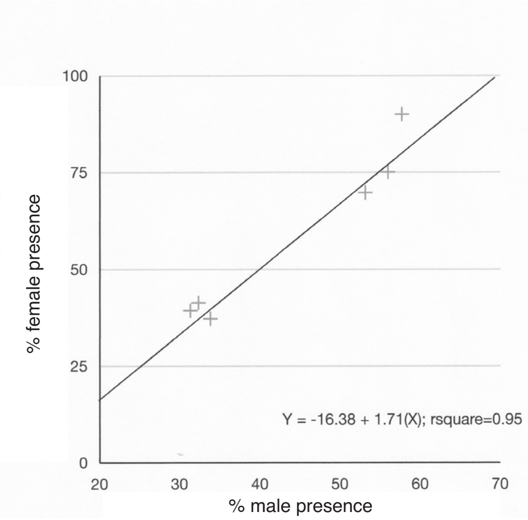

Figure 2. Female site fidelity (% of observation time in 5-day periods that the female was present at the site), against male site fidelity in the previous 5-day period (% of observation time that the male was at the site), in 1981, where Y= –16.38 + 1.71(X). Data are transformed using an arcsin transformation.

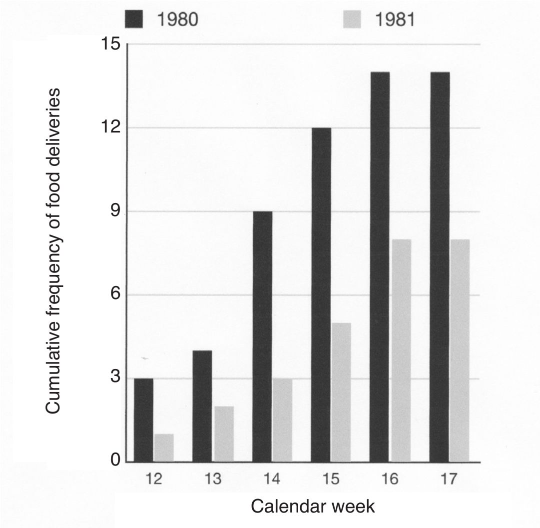

Figure 3. Cumulative frequency of food deliveries, against calendar week, in 1980 and 1981.

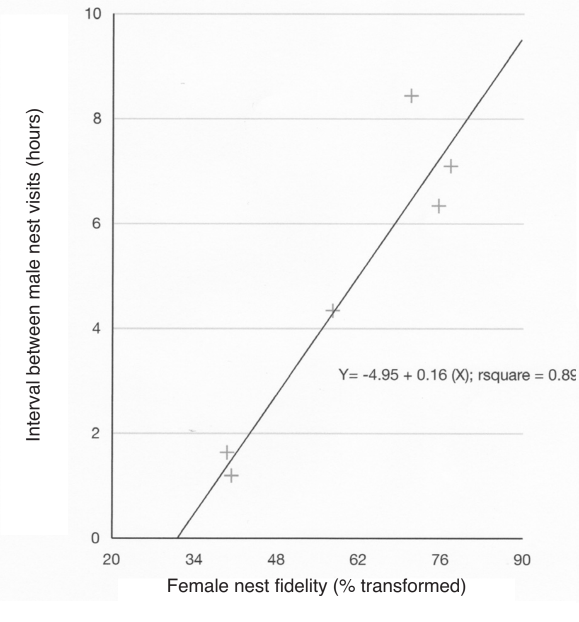

Figure 4. Interval between male nest visits (hours) against female nest fidelity (% of observation period that the female was on the nest) in the post-laying period, years combined; where Y= –4.95 + 0.16(X).

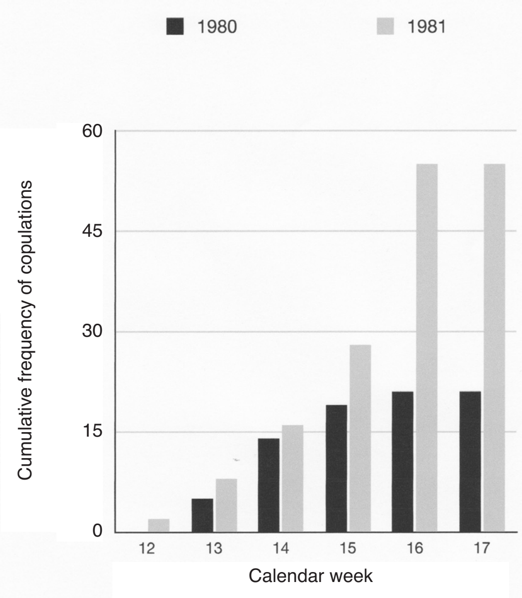

Figure 5. Cumulative frequency of copulations against calendar week for 1980 and 1981.

Table 3a. Frequency of Gyrfalcon courtship events (and average interval between occurrences in hours) by 5-day periods around the time of egg-laying.

Period	**M. Nest visit**		**F. Nest visit**		**M. Aerobatic**		**F. Aerobatic**	
	1980	**1981**	**1980**	**1981**	**1980**	**1981**	**1980**	**1981**
-5	1 (3.7)	4 (2.4)	0	1 (15.1)	1 (3.7)	2 (4.8)	1 (31.2)	1 (15.1)
-4	1 (8.2)	4 (2.8)	3 (10.1)	2 (9.1)	1 (8.2)	1 (11.3)	1 (30.4)	5 (3.7)
-3	7 (2.1)	2 (9.7)	1 (27.7)	0	3 (4.9)	2 (9.7)	1 (27.7)	1 (12.2)
-2	5 (4.8)	4 (1.8)	2 (12.5)	2 (10.1)	0	0	1 (24.9)	0
-1	14 (3.0)	3 (10.1)	16 (3.8)	5 (3.1)	1 (41.5)	2 (15.2)	1 (60.3)	2 (7.8)
0	5 (6.4)	9 (2.3)	8 (5.0)	5 (6.1)	14 (2.3)	0	3 (13.4)	1 (40.1)
1	4 (6.3)	11 (1.2)	6 (5.8)	9 (4.1)	3 (8.5)	5 (2.6)	0	8 (4.6)
2	9 (4.3)	5 (1.6)	11 (4.9)	4 (3.8)	5 (7.8)	3 (2.7)	6 (9.0)	2 (7.7)
3	1 (8.7)	0	2 (5.6)	2 (3.5)	0	0	1 (11.3)	0
4	1 (5.5)	1 (7.4)	1 (12.1)	2 (3.7)	3 (1.8)	0	0	0
Pre	28 (3.3)	17 (4.6)	22 (7.9)	10 (1.1)	6 (15.4)	7 (11.1)	5 (34.9)	9 (1.2)
Lay	5 (6.4)	9 (2.3)	8 (5.0)	5 (6.1)	14 (2.3)	0	3 (13.4)	1 (40.1)
Post	15 (5.2)	17 (1.8)	20 (5.6)	17 (2.0)	11 (7.1)	8 (3.7)	7 (16.0)	10 (3.4)
TotL	48 (4.2)	43 (2.3)	50 (6.5)	32 (2.0)	31 (6.5)	15 (6.7)	15 (21.8)	20 (3.3)
NonL		35 (2.9)		29 (1.4)		38 (2.6)		21 (1.9)
TOT	48 (4.2)	78 (2.9)	50 (6.5)	61 (1.7)	31 (6.5)	53 (4.3)	15 (21.8)	41 (2.6)

Table 3b. Frequency of Gyrfalcon food deliveries and copulations (and average interval between occurrences in hours) by 5-day periods around the time of laying.

Period	**Food drop**		**Copulations**	
	1980	**1981**	**1980**	**1981**
-5	1 (35.2)	0	0	3 (3.2)
-4	1 (51.7)	1 (41.7)	0	4 (2.8)
-3	1 (39.1)	1 (30.3)	3 (4.9)	6 (3.2)
-2	2 (18.0)	1 (23.0)	7 (3.4)	1 (7.1)x
-1	4 (16.4)	0	8 (5.2)	2 (15.2)
0	2 (20.3)	0	3 (10.6)	2 (10.5)
1	1 (40.3)	0	0	8 (1.7)
2	1 (53.8)	0	0	3 (2.7)
3	1 (11.3)	1 (6.9)	0	0
4	0	0	0	0
Pre	9 (25.3)	3 (57.1)	18 (5.1)	16 (4.9)
Lay	2 (20.3)	0	3 (10.6)	2 (10.5)
Post	3 (39.1)	1 (68.9)	0	11 (2.7)
TotL	14 (27.5)	4 (67.7)	21 (9.65)	29 (4.4)
NonL		4 (48.6)		26 (3.8)
TOT	14 (27.5)	8 (58.1)	21 (9.7)	55 (4.2)

Period = 5-day period around laying where 0 = laying
Pre = Pre-laying period
Lay = Laying period
Post = Post-laying period
TotL = Total of those pairs that laid eggs
NonL = Total of those pairs that failed to lay eggs
TOT = Total of all pairs observed

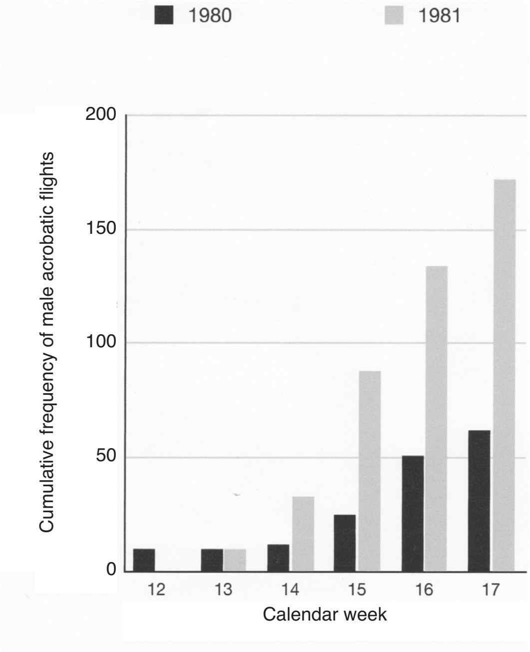

Figure 6. Cumulative frequency of male acrobatic flights against calendar week, in 1980 and 1981.

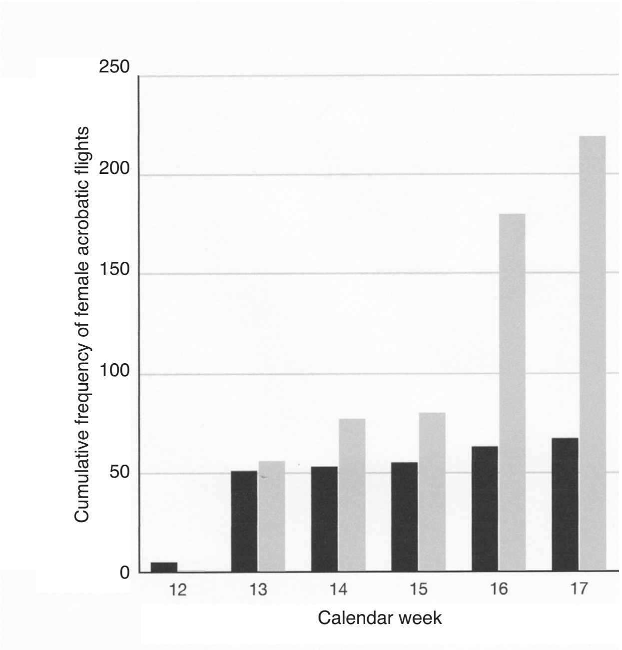

Figure 7. Cumulative frequency of female acrobatic flights against calendar week, in 1980 and 1981.

and 77.3 h. In the pre-laying period, early layers were provisioned with food every 16.6 h, in comparison to progressively later layers who received food every 26.0 and 63.5 h.

Nest Visits.—The frequency and pattern of male nest visits varied between years. In 1980, male nest visits were more common in the prelaying period (occurring every 3.3 h that he was at the site) than in the post-laying period (5.2 h per visit)(Table 3). This pattern was reversed in 1981, when male visits were more evident in the post-laying period (every 1.8 h) as compared to the pre-laying period (every 4.6 h). Overall, male nest visits were more common in 1981 (78) than in 1980 (51).

Male nest visits in the post-laying period may have been prompted by the female's restlessness. During the post-laying period across years, male visits were associated with the females' persistence on the nest. In a linear regression analysis, 89% of the variation in male nest visits was explained by the proportion of time the female remained on the nest (Figure 4). The female's apparent reluctance to remain on the nest in the post-laying period in 1981 (she was on the nest and attending the eggs only 52% of the time she was observed), may have been influenced by the male's fidelity to the site (he was present during only 43% of the post-laying period in 1981, as compared to 67% of the time in the previous year), or his inability to feed her during this period when she was recovering from egg-laying (only one food drop was observed in 70 h of observation in this period in 1981).

Nest visits varied with eventual reproductive success (see Table 2). Male nest visits were more frequent at sites that did not yield eggs (on average every 2.8 h), and at sites where eggs were abandoned (every 3.2 h) than at sites which successfully fledged young (every 5.3 h). Female nest visits followed the similar pattern; every 4.6, 5.7, and 7.2 h at non-breeding, abandoned, and successful sites, respectively. At one site, which fledged young in 1980 and failed to lay in 1981, the male visited that nest on average every 5.0 h in 1980 and every 2.8 h in 1981, while female visits occurred every 6.4 and 4.3 h in 1980 and 1981.

Females were less faithful to nests where the outcomes were poor. Overall, females were on eggless nests only 30% of the time they were at the site, and on nests that were eventually abandoned only 35.3% of the time, but where nests were successful, the female remained on the nest 78.5% of the time she was present at the site. Even in the pre-laying period, it was evident that the female was less loyal to nests that eventually failed—she remained on the nest 13.9% of the observation period at nests that were eventually abandoned as compared to 19.7% of the time on successful nests.

Nest visits and time spent on the nest also differed between laying date classes, with more frequent visits but shorter stays as laying was delayed. There were increasing male nest visits (every 4.0, 3.8 and 3.1 h) as laying was delayed, and shorter lengths-of-stay on the nest by females as laying was delayed. Females from early nests were present on the nest 57.9% of the time they were at the site, compared to 37.7 and 16.0% of site-time from the two later laying classes.

A general pattern of nest visitation was evident—more visits and shorter stays on the nests as laying was delayed and reproductive success was less assured—and therefore more evident in 1981 than in 1980.

Copulations.—Combining years, the first copulation was observed 24 days prior to laying, and the last, 12 days after laying. In 1980, copulations were first observed 14 days prior to laying and were frequent in the 10 days prior to laying (on average every 3.4 h while the pair were at the cliff together). In this year (1980), no copulations were observed in the post-laying period.

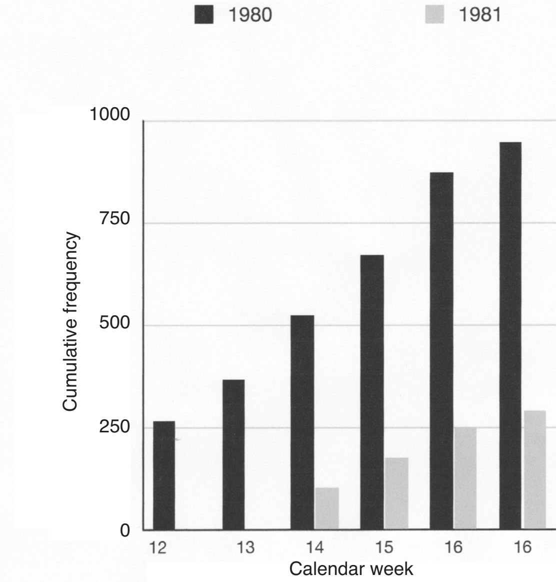

Figure 8. Cumulative frequency of mutual encounters, by year.

There was a tendency for copulations to occur less frequently and spanning fewer days when food was plentiful (1980) as compared to when food was scarce (1981) (Figure 5). During approximately 385 h of observation in each year, there were 21 copulations in 1980, and 55 in 1981. In 1980, the frequency of copulations (in 5-day periods) was linked to the frequency of food drops (r=0.85), a pattern not observed in 1981. In 1980, nearly all of the observed copulations occurred within a 10 day period before laying, in contrast to 1981 when copulations continued well after laying had commenced.

More copulations that extended over a longer period were also observed at failed (every 3.8 h) and delayed nests (every 6.4 h), in contrast to sites that fledged young (every 39.2 h). The difference was exaggerated in the pre-laying period—copulations at abandoned sites occurred every 6.9 h, and from successful sites, every 23.5 h (see Table 2). Copulations continued after laying at unproductive sites (every 4.9 h), and at those where laying was delayed (>20 April; every 3.8 h). This was in sharp contrast to pairs from productive sites and where laying was early; here copulations were halted after laying. Considering the entire observation period at one site between years, copulations occurred every 30.0 h when the pair was successful (1980) and every 5.9 h when they were unsuccessful (1981).

Aerobatic Displays.—Aerial displays by the male accounted for 60% of all aerobatic flights observed. Male aerobatic flights were often associated with nest visits, copulations, and female aerobatic displays. This was particularly pronounced in 1981—83% of all male aerobatic flights in 1981 were accompanied by a nest visit, copulation, or female aerobatic flight, compared to 58% in 1980.

In both years, male aerobatic displays were observed well in advance of laying and at similar frequency until about the middle of April at which time there was a dramatic increase in the number of aerobatic flights in 1981 which was not evident in 1980 (Figure 6). Altogether, 51 aerobatic flights were performed by the male while he was present at the site in 1980 (214 h), compared to 78 in 1981 over a similar observation period (210 h).

The frequency of male aerobatic displays varied with Gyrfalcon reproductive success and laying date. Males from sites that failed to lay eggs engaged in aerobatic flights on average every 5.1 h, in contrast to abandoned and successful sites who displayed aerial aerobatics every 10.1 and 10.7 h (see Table 2). The duration of male aerobatic flights also increased with decreasing reproductive success, and was most apparent in the post-laying period; males from abandoned nests spent 4% of the time in aerial aerobatic flights, while males from successful sites were airborne only 0.4% of the time. The time spent engaged in aerobatics also increased with delays in laying, particularly in the post-laying period. Late-laying (after 20 April) males spent 7.8% of their post-laying activity budget engaged in aerial displays, in comparison to males from earlier-laying sites who spent 0.3 and 0.4% of their time in aerobatic flights.

Female aerobatics occurred less frequently than male aerobatics but were generally of longer duration. However, there was a marked difference in the frequency of female aerobatic flights between years, and across the observation period. In 1980, female aerobatic flights were observed only well in advance of laying, and only 67 flights were observed in 330 h that the female was at the site, while in 1981, female aerobatic flights continued over time and were frequent (219 flights in 311 h) (Figure 7).

Female aerobatic displays also varied with productivity and date of laying. Non-breeding females were engaged in aerobatic displays every 9.3 h, while females abandoning eggs displayed every 12.7 h, and productive females every 19.6 h. At the one site, in the productive year of 1980, the female engaged in aerial displays only every 12.8 h, while what appeared to be the same female, based on plumage characteristics, in the following, non-breeding year, displayed every 7.3 h. The frequency and duration of female aerobatics was greater from delayed nests, occurring every 12.2 h and accounting for 2.2% of the time females were at the site, compared to intervals that exceeded 23 h and represented less than 0.4% of the females' activity budget. This trend was revealed in both pre- and post-laying periods, but was most apparent in the post-laying period.

Mutual Encounters.—When one sex encountered another there was initially a series of low bows and excited vocalizations, as described in detail by Platt (1977), and Wrege and Cade (1977). This behavior was especially pronounced when visits occurred on the nest. The low bow and excited vocalizations ("e-chip") did not persist longer than about one minute when the pair was together.

There were many such mutual encounters and sustained visits in 1980 in the Ogilive Mountains. A total of 947 mutual ledge visits were observed in 385 h of observation in 1980 (Figure 8), and altogether the male and female were together 8.1% of the observation period. Far fewer mutual visits were observed in 1981—only 291 visits were observed in 465 h of observation (see Figure 8), and they remained together 2.3% of time observed.

DISCUSSION

Williams (1966) described courtship as a contest between male salesmanship and female sales resistance. I interpreted Gyrfalcon courtship accordingly, as a sequence of events largely designed to provide criteria to persuade the female to invest in a brood. By this mechanism, reproductive effort is halted if food resources (ptarmigan/territory quality) or male capabilities are inadequate. Such a shut-off mechanism may be of critical importance to a northern avian predator where the growing season is short and the cost of reproduction is high.

The role of the male Gyrfalcon during the nesting season is to provision the female and the brood with food during the incubation period and the early brood period (Muir and Bird 1984, Jenkins 1978, Poole 1987). It is likely that early in the breeding season the female must rely on courtship behavior to assess the abilities of the male, and the availability of food resources. The obvious cue would be his ability to provide food during the pre-laying period.

Courtship feeding was originally thought to serve as a symbolic function in strengthening the pair bond (Lack 1954). Revision of this view has suggested that courtship feeding may serve as an important source of nutrition for females during egg formation and incubation (Royama 1966). Numerous studies have substantiated this latter concept, including those on Common Terns (*Sterna hirundo;* Nisbet 1973, 1977, Morris 1986), Blue Tits (*Parus caeruleus;* Krebs 1970), and Sparrowhawks (*Accipiter nisus;* Newton 1979, 1986). Studies of terns and gulls (*Larus* spp.) suggest that courtship feeding provides the basis for mate choice by the female (Nisbet 1973, Taylor 1979, Kilham 1981, Niebuhr 1981, Wiggens and Morris 1986). Halliday (1978) suggested that, in species where male parental investment is high, female choice should be based to a large degree on the male's willingness and ability to invest in her offspring.

Olsen et al. (1998), in a study of male provisioning in Peregrine Falcons (*Falco peregrinus*), suggested that females use courtship feeding to gauge male provisioning ability and, if male provisioning rates are predictable, females will adjust their breeding response. Thus, females paired with good male providers had greater reproductive success. In another study that modeled female behavior and fat storage dynamics (Brodin et al. 2003), large female fat reserves in the early nestling period were believed to be essential for successful breeding, again underlining the importance of male provisioning.

For Gyrfalcons, Platt (1977) found food transfers to be common in wild and captive pairs. He suggested they function as a mechanism to bring mates together. What he interpreted as begging, and a female behavior interpreted as "pushing" the male away from the nest site to hunt, were commonly observed in the wild. It was evident in my study, however, that food-provisioning rates were linked to general prosperity. In a year of high ptarmigan density and consequently high Gyrfalcon productivity, provisioning rates were 2.7 times higher than in a food-poor year when Gyrfalcon productivity was low. Irrespective of year, provisioning rates were higher at successful sites, and at sites nesting early. Laying date was closely correlated to productivity, both of which were linked to ptarmigan density which was over three times higher in 1980 than in 1981 (Barichello and Mossop 2011). Male provisioning rates appeared to provide a reliable indication of male fitness, and they were the most evident element of courtship. This pattern is consistent with the results of research on Sparrowhawks (Newton 1986), Ferruginous Hawks (*Buteo regalis*) (Powers 1980), terns (Nisbet 1977, Morris 1986, Taylor 1979, Kilham 1981, Wiggens and Morris 1986), and gulls (Niebuhr 1981).

Even so, Gyrfalcon courtship is not a single activity, but a series of events, including nest visits, animated aerobatic displays, vocalizations, and copulations. Fidelity to the breeding site, although not an ostentatious courtship activity, is a measure of attachment to the site or the mate. Attendance by the male permits him to perform for the female, as well as actively defend the site from other suitors. Frequent attention by the male may facilitate pair-bonding, and heighten the sexual drive, while providing the female with an assessment of the male. The risk of a female vacating the area in search of food or another mate is likely minimized if she is receiving frequent attention by the male.

I suspect two factors held the female to the nesting site—adequate food and male presence. Her faithfulness to the site prior to laying appeared to be influenced by food provisioning rates (apparent in both years), and the loyalty of the male to the site in the preceding 5-day period (particularly apparent in 1981). Infrequent food drops, compounded by male truancy, likely contributed to the lack of dedication by females to nesting sites in 1981, and coincided with eventual nest failures and delayed laying.

Although male Gyrfalcons attended sites less frequently when ptarmigan were less abundant, they showed no obvious tendency to compensate for fewer food deliveries by leaving the site to hunt more. In fact, the relationship between the calendar week and male presence at the site was remarkably consistent between years. I suspect absence from the nest site increased the risk that another male would contest the site. Its loss, for the resident male, would likely have severe consequences on his long-term reproductive success. The male's first priority, then, is likely the retention of a territory, for without a territory, high provisioning rates are of no consequence.

In most falcons, the nest appears to be of special significance (Newton 1979, Ratcliffe 1980, Walter 1979). Hagen (1952) found that male peregrines tried increasingly to lure females to a specific nest ledge, while Wrege and Cade (1977) found that five of ten courtship displays in large falcons were associated with the nest ledge. Similarly, Platt (1977) found much of the courtship activity of captive Gyrfalcons, including copulations, to be centered on the nest, and initiated by the male. Nest visits and associated behaviors probably serve to stimulate nesting behavior in the female.

Nest visits by male and female Gyrfalcons appear to be induced by different cues. I suspect photoperiod provides the initial stimulus for male nest visits, but thereafter nest visits are likely prompted by female behavior, including her interest in the nest and her apparent anxiety. The female's commitment to the nest and indeed, her level of unwillingness were likely influenced primarily by food—fewer food deliveries were associated with less persistence on the nest. This in turn led to frequent male nest visits. Not surprising then, male nest visits and female nest truancy were more common in the food-poor year (1981), and from unproductive and delayed nests. Mutual ledge visits might have been another indication of female restlessness. In 1981, female Gyrfalcons tolerated many fewer visits from the male (291 compared to 946 in the previous year) and they were together much less often (8.1% vs. 2.3% of the observation period).

Copulations and aerial aerobatic displays are very pretentious courtship gestures, generally accompanied by "excited" vocalizations. Gyrfalcon copulations in the wild have been reported to occur up to 39 days before clutch initiation. In Peregrines (Wrege and Cade 1977, Ratcliffe 1980) and in Kestrels (*Falco sparverius;* Willoughby and Cade 1964), copulations also occurred over a much longer period and more often than necessary for fertilizing eggs. Newton (1979) and Platt (1977) suggested that copulations serve as pair-bonding behavior, while Cade (1960) suggested they help synchronize the reproductive physiology of the pair. Either way, copulations serve a role beyond insemination.

In my study, Gyrfalcon copulations varied in frequency and intensity between years. When things were good (ptarmigan were abundant), and therefore Gyrfalcon food-provisioning rates were high and production was at its best, copulations were frequent but spanned a brief period directly before laying, presumably synchronized with reproductive physiology as suggested by Cade (1960). However, a year later, coinciding with a significant decline in the abundance of ptarmigan, copulations were altogether more frequent and extended well past laying, clearly serving a function beyond insemination. Presumably copulations, in addition to insemination, serve to motivate the female, and possibly reinforce the pair bond.

Aerial flights also appear to have more than one function. Platt (1977) classified five aerial displays during Gyrfalcon courtship, which closely resembled courtship flights described for Peregrines (Cade 1960, Wrege and Cade 1977, Nelson 1978), and suggested these were performed largely by the male to draw the female's attention to himself and the eyrie. Cade (1960) suggested that these display flights were modifications of hunting movements and territorial aggression designed to show the female his flying abilities.

The number and timing of Gyrfalcon aerobatic flights in my study varied from one year to the next. When times were good (1980) male aerobatics were most evident in the week of laying, then tailed off, and female aerobatics were evident only well in advance of laying. A year later when the ptarmigan population crashed, male aerobatics were few during the period of laying but frequent well past the laying period. Similarly, female aerobatics were more common than in the previous year and most evident after laying.

I suspect Gyrfalcon aerial aerobatic displays are designed to coax the female to the nest and stimulate sexual activity, using skills that emulate desirable traits, but also to advertise the occupancy of the site. When food is readily available and alternative mechanisms for seduction are generally unnecessary, aerobatic flights are performed only in the weeks leading up to and during laying. During the laying period, when the female enters a lethargic phase in order to manufacture eggs and begin a clutch, she may be particularly sensitive to disturbances that would interrupt the development of eggs. Advertisement by the male during this delicate period may minimize the risk of another Gyrfalcon or Golden Eagle entering occupied airspace.

*Summary.—*Although courtship unfolded as a drama of displays and vocalizations, a definite pattern emerged. A combination of photoperiod, physiology, and mate behavior likely influenced courtship activity. Female nest behavior appeared to be prompted largely by the rate at which the male provisioned her with food. Whether direct or indirect, this action provided a means to evaluate the male. Her stimulation to nest may come from the actual ritual of food transfer, or physiologically through weight gain or appetite-satiation levels. A poorly-fed female responded in a manner inappropriate to nesting. She was less loyal to the site and the nest, and displayed restlessness at the site through frequent aerobatic flights and infrequent mutual visits. Possibly this restlessness is an attempt to stimulate the male, or "push" him to hunt as interpreted by Platt (1977).

The male must convince the female to stay, and he must entice her to the nest. Although food provisioning appears to be the most alluring activity, other animated courtship displays –nest visits, copulations, and aerial displays– might serve to coax the female to nest, as well as play an important role in pair bonding and reproductive synchrony. They are likely employed to seduce passive females, and indeed, unresponsive females stimulate these displays. As with Ferruginous Hawks (Powers 1980), Gyrfalcon aerobatic flights appear to be infrequent when food-transfers are frequent.

Halliday (1978), suggested that there should be powerful selection for female coyness; that hesitant and cautious female responses should elicit more display from courting males, and therefore induce more evidence on which to discriminate. The increase in male "eagerness" may compensate for insufficient food drops, and may result in clutches being laid from poorly provisioned females. Intense male courtship displays, however, appear to be no substitute for food provisioning, as eventual nest failures were common from sites where advertising was frequent and provisioning rates infrequent.

Why then, would selection encourage these male courtship displays in addition to food provisioning? I offer two suggestions. The fact that eggs were laid from poorly provisioned, but intensively courted females, would give the pair at least a chance to fledge a brood, particularly if the resource base grew or became more vulnerable, as might be the case if the timing of ptarmigan courtship varied between years. Abandoning the nesting attempt early would forfeit any opportunity for producing young. Thus, despite poor provisioning rates, intensive courtship may be an advantage to induce egg-laying and the opportunity to adapt to environmental instability. Or, perhaps these courtship gestures may provide some indication of age and experience, and facilitate pair formation and bonding in food-poor years, when successful breeding, irrespective of the male's proficiency, is improbable. Pair formation and cooperation may be advantageous for hunting, as well as for future breeding attempts, giving the pair the necessary edge when ptarmigan are scarce, to remain on the nesting territory over the winter. Retention of a nesting territory is likely of critical importance to these long-lived falcons.

Courtship, then, provides an effective mechanism to allow the female to remain relatively inactive and gain weight prior to laying, while allowing her an assessment of the males' capacity to provide for a brood. This communication not only permits female discrimination, but enables the pair to abandon the reproductive effort early in the season when conditions are inappropriate and the probability of fledging a brood is small. The importance of female weight gain is consistent with the findings of Olsen et al. (1998) for Peregrines, and with the predictions of Brodin et al. (2003) that large female fat reserves in raptors, particularly in the first two weeks of the nestling period, are essential for successful breeding. This mechanism to adjust reproductive effort early in nesting cycle may be critical to these northern residents, whose over-winter survival may be in doubt if they proceed with the energy-demanding job of raising a brood whose survival is improbable in a year when ptarmigan are scarce. Courtship may also reinforce the pair bond, and so facilitate cooperation. This may be a decided advantage in enabling the pair to overwinter and retain a nesting territory, thereby guaranteeing them future breeding opportunities.

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