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Gyrfalcon Feeding Behavior during the Nestling Period in Central West Greenland

TRAVIS L. BOOMS[1] and MARK R. FULLER[2]

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ABSTRACT. We studied gyrfalcon (*Falco rusticolus*) food delivery and feeding behavior during the nestling period in central West Greenland during the 2000 and 2001 field seasons. We used time-lapse video cameras installed at three nests to record 2677.25 hours of nestling video. Ptarmigan delivered to nests were usually plucked prior to delivery and included the breast and superior thoracic vertebrae. Arctic hare leverets were rarely plucked and often delivered in parts. The most commonly delivered leveret part was the hind legs attached to the lower back. Passerines were rarely plucked and usually delivered whole. After feeding the young, adults removed 20.9% of prey items from the nest, which included items both with and without obvious muscle still attached. Prey delivery rates were similar among nests and increased as nestlings aged. Prey delivery frequency peaked in the morning and evening, with a distinct lull in the late evening and early morning hours. Male and female adults delivered a similar number of prey, though males typically delivered smaller prey than females. Gyrfalcons cached and re-delivered at least 9.1% of all items delivered, and one item was cached and retrieved three times.

Key words: camera, falcon, *Falco rusticolus*, feeding behavior, food habits, Greenland, gyrfalcon, time-lapse video

RÉSUMÉ. Durant les campagnes sur le terrain de 2000 et 2001 dans le centre du Groenland occidental, on a étudié chez le faucon gerfaut (*Falco rusticolus*) l'apport en nourriture et le comportement alimentaire pendant le séjour au nid. À l'aide de caméras vidéo filmant à intervalles, installées à trois nids, on a enregistré 2677,25 heures de vidéo au nid. Les lagopèdes apportés au nid étaient en général plumés avant d'y être déposés et comprenaient la poitrine et les vertèbres supérieures du thorax. Les jeunes lièvres arctiques étaient rarement pelés et étaient souvent apportés en morceaux. La partie du levraut la plus communément apportée était les pattes arrière rattachées au bas du dos. Les passereaux étaient rarement plumés et étaient en général livrés entiers. Après avoir nourri leurs petits, les adultes enlevaient du nid environ 20,9 % des parties des proies, comprenant des morceaux qui pouvaient comporter ou non du tissu musculaire évident. Le rythme de l'apport des proies était semblable parmi les divers nids et augmentait avec l'âge des oisillons. La fréquence de l'apport des proies passait par un maximum le matin et le soir, avec une accalmie très nette tard dans la soirée et au petit matin. Les mâles et les femelles adultes apportaient le même nombre de proies, mais les mâles livraient en général de plus petites proies que les femelles. Les faucons gerfauts dissimulaient dans une cache puis ressortaient par la suite au moins 9,1 % de tous les morceaux apportés, et un morceau a été dissimulé et ressorti trois fois.

Mots clés: caméra, faucon, *Falco rusticolus,* comportement alimentaire, habitudes alimentaires, Groenland, faucon gerfaut, enregistrement vidéo à intervalles

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INTRODUCTION

The gyrfalcon (*Falco rusticolus*) is a circumpolar raptor inhabiting Arctic and Subarctic landscapes above 60˚ N latitude. It is an apex predator and may serve as an indicator of the health of the landscapes in which it occurs. However, the remoteness of its extreme northern distribution, combined with its uncommon status, has prevented scientists from studying many aspects of its ecology and life history (Clum and Cade, 1994). This is especially so for gyrfalcons in central West Greenland; Cade et al. (1998:1) found that, in comparison to other regions, "fresh data from Greenland and Russia lag far behind."

As part of a study on Greenland gyrfalcon diet (Booms and Fuller, 2003), we used time-lapse video photography to document prey items delivered to gyrfalcon nests throughout the nestling period (hatching to fledging) during the 2000 and 2001 breeding seasons. While the cameras recorded delivery of prey items, they also recorded the birds' feeding behavior at nests. We analyzed the video to study the feeding behavior of nesting gyrfalcons, and this paper reports those results.

Gyrfalcon feeding behavior has previously been investigated by direct observations using binoculars and scopes, typically placed 200–400 m from the nest (Poole and Boag, 1988), or with Super-8 time-lapse cameras (Jenkins, 1978). However, observer effects on nesting gyrfalcons are difficult to ascertain. Muir and Bird (1984) noted that their presence in observational blinds might have caused an adult male gyrfalcon to abandon its nest. Woodin

[1] Boise State University Raptor Research Center, 1910 University Drive, Boise, Idaho 83725, U.S.A.; present address: N10909 Oxbow Ln., Wausaukee, Wisconsin 54177, U.S.A.; travisbooms@hotmail.com
[2] USGS Forest Rangeland Ecosystem Science Center, 970 Lusk St., Boise, Idaho 83706, U.S.A.

(1980) also documented potential observer effects while studying gyrfalcons, noting that adults would not tolerate his presence within 250–500 m of the nest. Conversely, Poole and Boag (1988), who observed gyrfalcons for 801 hours during pre-nesting and nesting, did not mention any such effects.

Cameras installed at gyrfalcon nests might cause less observer effect than conventional direct observations. Jenkins (1978) noted no apparent camera effects on nesting gyrfalcons in Greenland when using a Super-8 photography system, though the birds' behavior was influenced temporarily while he was changing film at the nest. Enderson et al. (1973) used the same time-lapse system and also found no evidence of camera effects on nesting peregrine falcons (*Falco peregrinus*). However, Jenkins (1978) and Tømmeraas (1989) experienced camera failures with Super-8 systems, and Jenkins (1978) found that the exposure rate of one frame every 60 seconds was too slow to document short behaviors, such as brief feeding events. Tømmeraas's (1989) camera system sampled behavior even less frequently, exposing one frame every eight minutes. Recently, video recording was useful for obtaining regular documentation of food deliveries to northern goshawk (*Accipter gentilis*) nests in the temperate rain forests of southeast Alaska (Lewis et al., in press).

Our understanding of gyrfalcon feeding behavior to date rests principally on a small body of literature. Some of these studies observed only a fraction of the nestling period (Fletcher and Webby, 1977, 40 hours; Poole and Bromley, 1985, 68.5 hours), and studies using Super-8 time-lapse camera systems potentially missed important, albeit short, behaviors (Jenkins, 1978; Tømmeraas, 1989). Three sources describe gyrfalcon nesting behavior during the nestling period with continual observations for a longer period. Platt (1989) made observations during 24 days from a blind at two gyrfalcon nests in the Yukon Territory, Canada. Bente (1981) observed two gyrfalcon nests for 538.4 hours, which included incubation, nestling, and post-fledging periods. Poole and Boag (1988) provided the most authoritative account of gyrfalcon nesting behavior. They observed gyrfalcon nests in the central Canadian Arctic for 801 hours and recorded behavior at seven nests with time-lapse, Super-8 cameras.

This paper describes gyrfalcon food delivery and feeding behaviors recorded at nest sites using modern time-lapse video equipment. We extracted data from 2677.25 hours of nestling video taken at three nests in central West Greenland. To our knowledge, this is the largest compilation of observation hours used to analyze nesting gyrfalcon feeding behavior, and we hope these data enhance current knowledge of this little-studied species.

STUDY AREA

The study area, located in central West Greenland, was originally established by W. G. Mattox during the Greenland Peregrine Falcon Survey (Mattox and Seegar, 1988). The area covers approximately 7000 km^2 and is located just north of the Arctic Circle. It extends 80 km from south to north (66˚45′ to 67˚30′ N) and 85 km from east to west (49˚55′ to 52˚05′ W). The only town in the study area, Kangerlussuaq, served as our permanent base of operations.

The habitat is mountainous, treeless tundra with many cliffs up to 200 m in height and elevations up to 880 m. It contains numerous small lakes and supports a simple faunal community (Burnham and Mattox, 1984). The floral community consists primarily of low-growing willow (*Salix* spp.) and dwarf birch (*Betula nana*), sedges (*Carex* spp.), and grasses. Mammals include the arctic fox (*Alopex lagopus*), arctic hare (*Lepus arcticus*), Greenland caribou (*Rangifer tarandus*), and muskox (*Ovibos moschatus*). No rodents occur in the area. Thirty bird species have been observed, though only 18 species are considered common (Burnham and Mattox, 1984; Meese and Fuller, 1987). Gyrfalcons, peregrine falcons, white-tailed eagles (*Haliaeetus albicilla*), and common ravens (*Corvus corax*), all of which nest on cliffs, are the only avian predators in the study area.

The low Arctic climate is continental, with large temperature extremes and little precipitation (annual mean = 15 cm). Weather was similar during our 2000 and 2001 field seasons. Being north of the Arctic Circle, the study area experiences continuous daylight from the middle of May through the beginning of August. For a more detailed description of the study area, see Burnham and Mattox (1984).

METHODS

We monitored two different gyrfalcon nests each year during the 2000 and 2001 field seasons with time-lapse recording units. In 2000, we installed a camera at one nest during late incubation and another at a second nest when young were approximately five days old. In 2001, we installed both cameras during mid-incubation. Only the video shot during the nestling period from both years was used for analysis. After installation, we changed tapes daily or as logistics allowed until the first young fledged (first flew from the nest ledge). Because the nest ledges were relatively small and nestlings were confined to the area viewed by the camera, very few prey deliveries were missed.

We monitored nests with separate Sentinel All-Weather Video Surveillance Systems from Sandpiper Technologies, Inc. Each system included a small camera, a VCR, and connecting cables. The cameras were installed within 2 m of the nests and connected by cable to all other equipment, which was located at the top or bottom of the nest cliff. This allowed us to change tapes while not noticeably disturbing birds on the nest (we confirmed this by watching adults' behavior on the video during tape changing events).

The camera was a PicoCam miniature video color camera measuring 5.5 × 4 × 4 cm (L × W × H) made by Watec

Corporation. We used a Sony SVT-DL224 time-lapse VCR that recorded 20 frames per second (one-third real time), allowing 24 hours of recording on one T-160 videotape.

The Sentinel Systems were powered by solar panel arrays that delivered power to a battery bank. The system contained two 100-watt, 12-volt, Siemens SR100 photovoltaic modules. We used three Deka 12-volt, 98-amp gel cell sealed batteries for each system to store the energy produced by the solar panels and to supply power to the VCR. When fully charged, the battery bank could power the VCR and camera for 3.5 days in case of prolonged periods of low solar radiation. We present a detailed description of the video system elsewhere (Booms and Fuller, in press).

After each field season, we viewed all videocassettes on a 68 cm color television, played in fast-forward mode in the same Sony VCR used to record them. We continued to fast-forward through the tape until we observed a food delivery. We then played the sequence at regular speed and recorded pertinent information about the prey item and behavior during each food delivery. If necessary, we played the delivery sequence frame by frame until we either identified the prey item or deemed it unidentifiable.

We quantified the minimum number of prey individuals delivered to each nest by dealing with intact and dismembered items separately. For those items delivered whole or headless, we summed the total number of items delivered to each nest. When items were delivered in separate, dismembered parts during 24 hours (as was sometimes the case with arctic hares), we tallied the delivered parts until they represented one individual prey animal. We then regarded those deliveries collectively as one individual, thereby minimizing inflated prey counts.

We used adult and juvenile prey biomass estimates taken from field collections and those reported in Schaanning (1933), Johnsen (1953), Prestrud and Nilssen (1992), Dunning (1993), and Rosenfield et al. (1995). We estimated leveret age from an average parturition date observed each year and then applied a growth curve (Parker, 1977) to estimate leveret biomasses.

The fact that adults cache prey items and deliver the same item a second time can artificially inflate total prey counts. To reduce error, we recorded the condition of prey items upon delivery and removal (if adults removed the item after feeding). If a delivered prey item looked like an item recently removed from the nest, we considered the item as “retrieved” from a cache and did not record it as a new individual. Though the method was not foolproof, because adults could alter the appearance of an item by feeding on it themselves after removing it from the nest, this conservative approach to redelivered items likely eliminated most double counts.

All analyses are of unpooled data from three successful nests, unless otherwise stated. Unfortunately, the fourth video-monitored nest failed in 2001, two days after the young hatched. Two young rolled off the badly sloping nest ledge when adults nestled down to brood, while the third died from unknown causes in the nest. Therefore, we did not use data from this nest in any analyses or summaries.

We recorded 2677.25 hours of videotape from the three successful nests, covering an average of 77.2% of the entire nestling period for each nest. For frequency analyses, we excluded 220 hours of videotape from days during which the gyrfalcons were disturbed by our extended presence (while banding young and installing video equipment) and days during which we did not record all 24 hours because of mechanical failures or logistical constraints. These occasional lapses in coverage were distributed throughout the nestling period, so any potential temporal bias caused by excluded data is minimal.

We used the log likelihood ratio test to compare hourly delivery rates with a uniform 24 h day distribution. Because all data sets for regression and ANOVA analyses failed the assumption of normality or equal variances or both, we used nonparametric equivalents. We used Spearman rank correlation to look for relationships between nestling age and the number of deliveries per day, the amount of biomass delivered per day, and the average biomass per prey item. We looked for differences among nests in length of feeding bouts, using the Kruskal-Wallis test. We judged all results significant at the $\alpha = 0.05$ level.

Throughout the paper, we use the following definitions: a *prey item* is any piece of food delivered to a nest, including whole prey and individual dismembered prey parts; *feeding* involves an adult’s removing a piece of food from a prey item and placing it in a nestling’s mouth; a *feeding bout* is the time spanning the first and last piece of food placed in any nestling’s mouth by an adult from an individual prey item (nestlings eating prey unassisted by the adult does not qualify as a feeding bout); *food delivery* involves an adult bringing a prey item to the nest, regardless of whether an adult feeds the item to the young or the young consume the item unassisted by an adult; and *leaving prey* is an adult’s dropping a prey item at the nest without feeding young. The young then consume the prey item unassisted by an adult.

RESULTS

Food Handling

The vast majority of items (99.5%; n = 832) delivered to gyrfalcon nests and identified to the order level or lower belonged to one of three prey item categories: adult rock ptarmigan (*Lagopus mutus*) (juvenile ptarmigan were not present during the gyrfalcon nestling period), arctic hare young of the year (hereafter leveret), or passerines.

Gyrfalcons plucked 96% of the ptarmigan they delivered to nests (n = 207, excluding items retrieved after caching). Most were completely denuded of all feathers, except a few distal primaries. Only seven individuals appeared unplucked, with all feather tracts visibly intact. Ptarmigan breasts with superior thoracic vertebrae at-

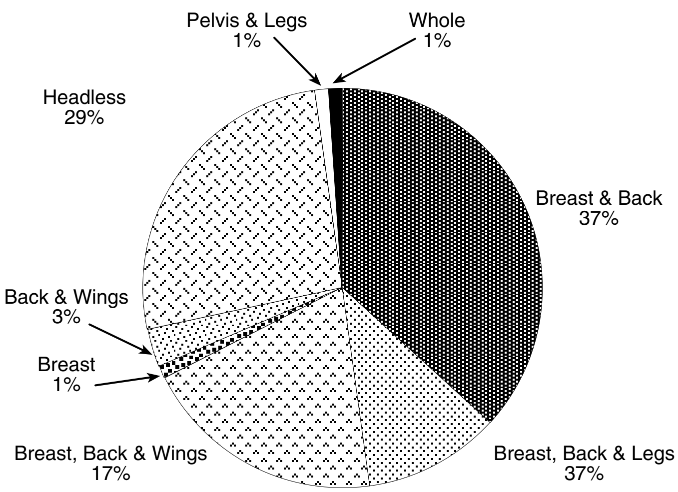

FIG. 1. Description of ptarmigan food items delivered to three video-monitored gyrfalcon nests in West Greenland in 2000 and 2001.

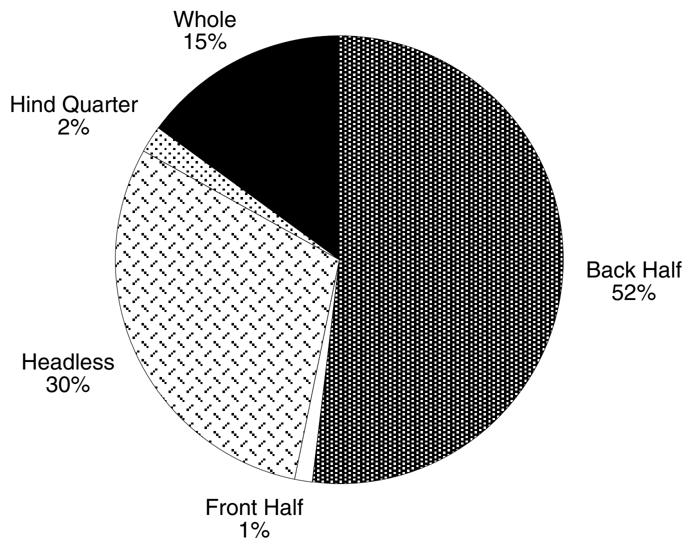

FIG. 2. Description of arctic hare leveret food items delivered to three video-monitored gyrfalcon nests in West Greenland in 2000 and 2001.

tached were the most common ptarmigan item delivered, sometimes with wings also attached (Fig. 1). The organs from the thoracic cavity were usually missing when ptarmigan were delivered in this configuration. Gyrfalcons delivered headless ptarmigan nearly as often as the breast and back configuration, though in this case, the bird often was not eviscerated. In total, 33% of all the ptarmigan items delivered were noticeably partially eaten or dismembered before being brought to the nest. Feeding bouts on ptarmigan items lasted from 1 to 30 minutes, averaging 15.9 minutes (n = 205, SE = 0.43).

Gyrfalcons did not pluck most arctic hare leverets (86%; n = 122). The falcons typically delivered leverets in pieces, and the most common piece was the back half, consisting of the lumbar vertebrae, pelvis, and hind limbs (Fig. 2). However, small leverets (less than 600 g) were regularly delivered whole or headless. Like the ptarmigan items, 33% of the leveret items were partially consumed or visibly dismembered before delivery. The mean length of leveret feeding bouts was 10.0 minutes (n = 101, range 1–26 min, SE = 0.52). The size of the hares delivered to nests ranged from 325 to 1765 g and averaged 890 g (n = 122, SE = 31.62).

Gyrfalcons delivered 74% of passerines whole (n = 311); rarely were they visibly plucked (< 1%) or partially eaten (< 1%).

After feeding, the adult females removed nearly 21% of prey items from the nest, including items both with and without obvious muscle left attached, though removal rates varied among nests (Table 1).

Deliveries

The number of deliveries per day and the daily average prey item biomass were similar among nests (Table 2). The mean daily biomass delivered to each nest varied among nests: Nest 3 had the highest average daily amount, though it contained fewer nestlings than Nest 1. When corrected for the number of nestlings, including the female as a "nestling" (Poole and Boag, 1988), daily delivery rates and biomass delivered per nestling were higher in nests with fewer young (Table 2). The number of deliveries per day was positively correlated with nestling age ($r = 0.60$, $p < 0.001$). The amount of biomass delivered per day was also positively correlated with nestling age ($r = 0.22$, $p = 0.02$). However, the average item biomass decreased as nestlings aged ($r = -0.48$, $p < 0.001$).

Food deliveries were not uniformly distributed across a 24 hour day ($\chi^2 = 172.04$, df = 23, $p < 0.001$). The frequencies resembled a bimodal distribution, with peaks between 0700 and 1100 hours and between 1600 and 2100 hours (Fig. 3). There was a substantial decline in deliveries between 2100 and 2400 hours, followed by the lowest delivery frequencies from 0100 to 0400 hours. This trend held true when each prey category was examined individually (Fig. 4).

Feeding bouts lasted an average of 13.3 minutes (range 1–34 min, SE = 0.32, n = 437). We did not detect a difference in feeding-bout lengths among nests, regardless of the number of nestlings ($\chi^2 = 3.39$, df = 2, $p > 0.18$).

Adults began leaving prey at the nest when nestlings were 28, 35, and 38 days old at Nests 1, 2, and 3, respectively. Thereafter, adults routinely delivered passerines and small birds without feeding, though at Nests 2 and 3 most large items were fed to young through the end of the nestling period. At Nest 1, all feeding bouts stopped after nestlings were 40 days old.

Parental Roles

Overall, food deliveries appeared evenly distributed between male and female adults (females 43.5%, males

TABLE 1. Prey items removed from three video-monitored gyrfalcon nests in order of increasing numbers of removals.

Nest	Removed from Nest			Unknown	Not Removed	Total
	Edible Item[1]	Inedible Bones[2]	Total			
Nest 3	19	4	23 (12.6%)	6 (3.3%)	153 (84.1%)	182
Nest 1	20	12	32 (8.1%)	1 (0.2%)	360 (91.6%)	393
Nest 2	83	54	137 (39.6%)	0	209 (60.4%)	346
Combined	122	70	192 (20.9%)	7 (0.7%)	721 (78.4%)	921

[1] Items removed with visible muscle attached, not completely consumed.

[2] Items stripped of all visible, edible muscle.

TABLE 2. Average daily food deliveries at three video-monitored gyrfalcon nests.

Nest	Young[1]	Number of Deliveries/day				Biomass Delivered (g)/day				Prey Item Biomass (g)/day		
		Per Nestling	Mean	SE	Min, Max	Per Nestling	Mean	SE	Min, Max	Mean	SE	Min, Max
Nest 2	3	2.8	8.3	0.8	3, 24	665	1994.9	111.1	575, 3903	390.2	25.9	27.4, 743
Nest 3	4	2.1	8.5	1.2	3, 18	592	2368.9	254.1	1028, 4596	364.8	50.3	94.2, 766
Nest 1	5	1.7	8.4	1	1, 22	413	2065.2	189.9	250, 6106	386.8	28.9	27.4, 775
All			8.4	0.6	1, 24		2084.7	102.2	250, 6106	384.7	18.1	27.4, 775

[1] Number of nestlings in each nest, counting adult female as one nestling (Poole and Boag 1988).

46.8%, unknown 9.7% of pooled deliveries), though most food deliveries by males were of passerines during the second half of the nestling period. Again, variation among nests was high. The male at Nest 3 delivered only 15.3% of the prey items, whereas the male at Nest 1 delivered 62.8% of all items, almost double the percentage delivered by his mate (34.4%). Conversely, the females at all nests fed nestlings far more often than males did (females 97.7%, males 2.3% of 437 pooled feedings); thus, when males delivered items to the nest, they typically left the item in the nest and allowed the females to feed the young or the nestlings to feed themselves.

At least 84 prey items (representing 9.1% of the total number of items delivered) were removed from nests and subsequently redelivered, presumably after being cached. Females from Nests 1 and 2 delivered most of the retrieved items (Table 3). Most items were partially consumed ptarmigan or hare that the falcons delivered during the first two-thirds of the nestling period and removed after the nestlings were satiated. One item was cached and subsequently retrieved three times, though the majority of items were retrieved only once.

DISCUSSION

Food Handling

Langvatn (1977) provided a detailed description and quantification of the prey remains found at gyrfalcon nests. He admitted that extrapolating from the bones one finds as prey remains to the condition of prey at the time of delivery likely provides a biased view of food handling. He concluded that many prey items were likely brought to the nest intact, except for being decapitated and plucked.

Though this is what we found for passerines, most ptarmigan and hare were not delivered intact. Rather, 58% of ptarmigan deliveries were missing the lower back and legs, and 51% of leveret deliveries consisted of only the back half of the hare. We observed a leveret front half delivered to a nest only once. Cade et al. (1998) stated that adults often consume ptarmigan heads and legs near kill sites, though they offered no explanation for this behavior. Hagen (1952) reported that ptarmigan legs were common in adult gyrfalcon pellets, but not so in pellets from nestlings. Therefore, it seems that gyrfalcons may deliver only certain prey parts to the nest (ptarmigan breasts and leveret hindquarters in this study) and apparently eat the other prey parts outside the nest. This behavior could be motivated by (a) energetic costs related to flying with items to the nest (e.g., Pennycuick et al., 1989, 1990, 1994), (b) the greater nutritional value to nestlings of certain portions of prey, or (c) adult preferences for certain prey parts.

While we cannot refute explanations (b) and (c), our data support the idea that (a) energetic costs may at least partially explain the trends documented here. Leveret hindquarters and ptarmigan breasts are more compact and likely provide more meat per unit volume compared to the leveret's chest cavity and smaller front legs and the ptarmigan's bony lower back and legs. Leveret hindquarters and ptarmigan breasts also probably offer less aerodynamic resistance than bulky leveret front halves and dangling ptarmigan legs. Carrying objects during flight can increase power requirements for flight because of additional mass and aerodynamic drag (Obrecht et al., 1998; Pennycuick et al., 1988, 1989). Consequently, we speculate that adults repeatedly delivered similar prey parts to nests because they contained more meat and maximized transport efficiency.

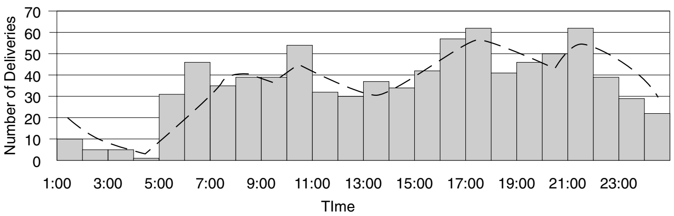

FIG. 3. Distribution of food deliveries per hour with three-hour moving average at three video-monitored gyrfalcon nests (pooled data).

Some studies of gyrfalcon food habits have described adults' removal from the nest of prey items, both inedible remains and items not completely eaten (Woodin, 1980). We documented this removal at all three nests, though differences among nests in the frequency of this behavior were large. The adults at Nests 1 and 3 removed only 8.1% and 12.6% of delivered prey items, including items that were apparently stripped of all meat and likely dropped elsewhere, as suggested by Bengtson (1971). Adults from Nest 2 removed 40% of all delivered items. Of the removed items, 39% were inedible bones. Removing inedible items appears to be an inconsistent behavior of gyrfalcons, because Platt (1989) observed no such behavior, and we documented large differences among nests.

Deliveries

The delivery rates we documented were higher than those reported by others, perhaps because of differences in diet or because previous estimates were from intermittent Super-8 film clips (Poole, 1988; Poole and Boag, 1988). The gyrfalcons in Poole and Boag's study (1988) relied more on larger prey items such as arctic ground squirrels (*Spermophilus parryii*) and less on passerines than the gyrfalcons we studied. Because adults must deliver more small items to equal the biomass afforded by one large item, it is logical that we documented higher delivery rates than Poole and Boag (1988). As Jenkins (1978) suggested, Super-8 film clips can also miss brief deliveries. Super-8 cameras used in Jenkins (1978) and Poole and Boag (1988) likely would have missed most passerine deliveries late in the nestling period in our study because they lasted only one to two seconds. This method would have falsely lowered our estimated delivery rates and made them closer to other published estimates.

The 13.3 minute mean feeding-bout length may be misleading in relation to deliveries potentially missed by Super-8 video. In this study, the vast majority of deliveries that would have been missed were not feedings, but rather cases in which adults left prey at nests and nestlings fed themselves. This occurred frequently after young were approximately 35 days old. Hence, the 13.3 minute mean feeding-bout length would lend support to the argument that Super-8 video recording at one frame every one to five minutes captures most feedings, but misses many deliveries when adults leave small prey items for older nestlings.

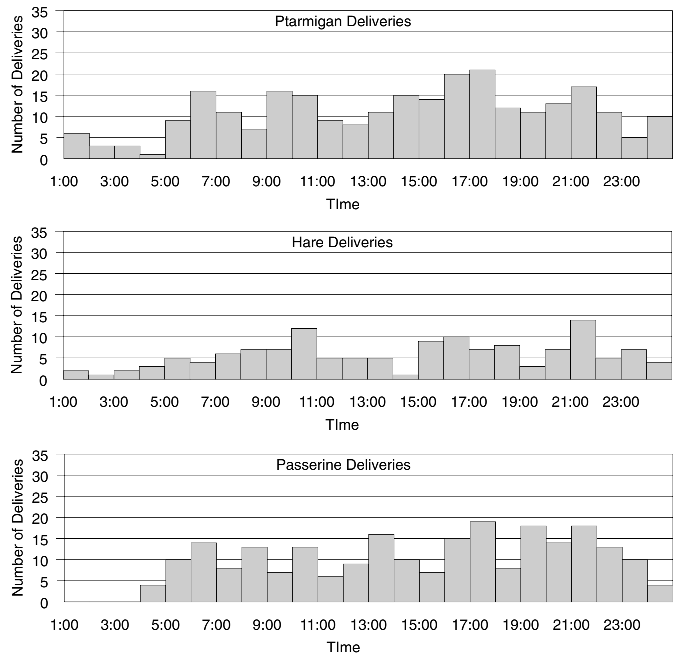

FIG. 4. Distribution of food deliveries per hour, by prey category, at three video-monitored gyrfalcon nests (pooled data).

An increase of passerine deliveries during the second half of the nestling period, together with nestling growth, likely caused the positive correlation between the number of deliveries per day and nestling age. These smaller prey items required more deliveries to provide the same biomass found in larger items. The negative correlation between the average prey item biomass and nestling age was also caused by the high number of passerines delivered late in the nestling period and by a corresponding reduction in ptarmigan and hare deliveries.

The distribution of deliveries during the day was similar to the pattern documented by Jenkins (1982), with the highest peak in delivery frequency in the evening, a slightly lower peak in mid-morning, and the lowest delivery rates in the early morning. Jenkins (1982) hypothesized that the periodicity of food deliveries in an environment where there is continuous light during the nestling period is likely related to prey activity, gyrfalcon hunting success, or activity patterns (i.e., circadian rhythms) or some combination of those factors.

We noticed that male rock ptarmigan became particularly active after 2300 hours and continued displaying on rocks, chasing or flying after conspecifics, and making aerial flight and call displays until the early morning hours. This period of increased ptarmigan activity coincided with a documented lull in food deliveries to gyrfalcon nests. If the temporal pattern of gyrfalcon food deliveries was influenced by prey activity cycles, we would expect a peak in deliveries between 2300 and 0300 hours, when ptarmigan, the primary prey species during May and June, seemed most active (assuming prey are most susceptible to predation when physically active). Conversely, the gyrfalcons delivered the fewest prey items

TABLE 3. Items retrieved from caches and redelivered to gyrfalcon nests.

Nest	Male[1]	Female[2]	Total Retrieved	Latest Retrieval[3]	Total Deliveries
Nest 1	0	22	22 (6.6%)	31	393
Nest 2	9	49	58 (16.8%)	42	345
Nest 3	0	4	4 (2.2%)	43	182
Totals	9	75	84 (9.1%)		920

[1] Number of retrieved items delivered by the adult male.
[2] Number of retrieved items delivered by the adult female.
[3] Age of nestlings (days) when adults stopped retrieving cached items.

during this time. We also would expect the delivery pattern to change as gyrfalcons focus on different prey species that may be active at differing parts of the day. When looking at delivery frequencies for rock ptarmigan, arctic hare, and passerines individually, in each case gyrfalcons exhibited a distinct lull in deliveries between midnight and 0400 hours (Fig. 4). Thus, though we base our conclusion solely on anecdotal field observations, we speculate that the distribution of food deliveries may not be influenced noticeably by prey activity cycles.

Parental Roles

There was wide variation in behavior among individual adults and adult pairs. From our field observations, females appeared to begin hunting and killing large prey items (leverets and ptarmigan) after the nestlings were about three to four weeks old. At the same time, young passerines began fledging and male gyrfalcons probably began specializing on these small, easily caught prey.

The camera did not record prey transfers outside the nest, so we could not substantiate identification of which parent killed what type of prey at Nests 2 and 3. We made extensive observations at Nest 1 during the last two weeks of the nestling period (concurrently with the video-recording of deliveries) in which we commonly observed the male perched on one of three hunting perches near or on the nest cliff. From these perches, the male made frequent slow, gliding flights to the valley below to catch passerine fledglings. During this time, we did not see the male flying with an item larger than a passerine, but we often observed the female flying into the nest with large prey items that we later identified on the video as leverets and ptarmigan. Hence, male and female hunting roles at Nest 1 appeared quite different near the end of the nestling period, with the male taking many fledgling passerines and the female taking a smaller number of comparatively larger leverets and ptarmigan. This trend likely held true at the two other nests, as most prey items delivered by males were passerines and most female deliveries were of ptarmigan and leverets.

When conducting research with limited resources on an uncommon Arctic species, one must study either a few birds intensively or many birds extensively. We chose the former method. Consequently, we cannot interpret the results as representative of gyrfalcons across the study area or throughout West Greenland. However, when our results are combined with those of similar studies from other areas, general trends emerge. Many of our results support and add to these trends. Most ptarmigan and hares documented here were not delivered whole and routinely missed certain body parts, suggesting that parents had specific food handling techniques, possibly to maximize transport efficiency. Delivery rates were higher than previously reported, though the distribution of deliveries during the day was similar to those recorded in other studies, with a distinct lull from late evening to early morning. We speculate that the distribution of deliveries was not influenced noticeably by prey activity cycles. Food delivery roles of male and female parents differed temporally and among nesting pairs. Males rarely fed nestlings and likely were responsible for all hunting during the first two weeks of the nestling period. Removal of prey and inedible remains from the nest varied among nesting pairs, as did apparent caching and redelivery of previously delivered items.

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