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GYRFALCON DIET IN CENTRAL WEST GREENLAND DURING THE NESTING PERIOD

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Abstract. We studied food habits of Gyrfalcons (*Falco rusticolus*) nesting in central west Greenland in 2000 and 2001 using three sources of data: time-lapse video (3 nests), prey remains (22 nests), and regurgitated pellets (19 nests). These sources provided different information describing the diet during the nesting period. Gyrfalcons relied heavily on Rock Ptarmigan (*Lagopus mutus*) and arctic hares (*Lepus arcticus*). Combined, these species contributed 79–91% of the total diet, depending on the data used. Passerines were the third most important group. Prey less common in the diet included waterfowl, arctic fox pups (*Alopex lagopus*), shorebirds, gulls, alcids, and falcons. All Rock Ptarmigan were adults, and all but one arctic hare were young of the year. Most passerines were fledglings. We observed two diet shifts, first from a preponderance of ptarmigan to hares in mid-June, and second to passerines in late June. The video-monitored Gyrfalcons consumed 94–110 kg of food per nest during the nestling period, higher than previously estimated. Using a combination of video, prey remains, and pellets was important to accurately document Gyrfalcon diet, and we strongly recommend using time-lapse video in future diet studies to identify biases in prey remains and pellet data.

Key words: camera, diet, Falco rusticolus*, food habits, Greenland, Gyrfalcon, time-lapse video.*

Dieta de *Falco rusticolus* durante el Período de Nidificación en el Centro-Oeste de Groenlandia

Resumen. Estudiamos los hábitos alimenticios de *Falco rusticolus* durante la época de nidificación en el centro-oeste de Groenlandia durante los años 2000 y 2001. Utilizamos tres fuentes de datos: registros en lapsos de tiempo con cámaras de video (nidos en los árboles), restos de presas (22 nidos) y egagrópilas (19 nidos). Esto permitió describir la dieta durante el período de nidificación con base en la información diferente provista por cada fuente. *F. rusticolus* dependió fuertemente de las presas *Lagopus mutus* y *Lepus arcticus*. En forma combinada, estas dos especies contribuyeron en un 79–91% de la dieta total, dependiendo de los datos utilizados para el análisis. Las aves paserinas fueron el tercer grupo más importante. Las presas menos comunes presentes en la dieta fueron aves acuáticas, cachorros de zorro (*Alopex lagopus*), aves playeras, gaviotas, álcidos y halcones. Todos los individuos de *L. mutus* fueron adultos y todos excepto un individuo de *L. arcticus* fueron juveniles nacidos ese mismo año. La mayoría de las aves paserinas fueron volantones. Observamos dos cambios en la dieta, primero de preponderancia de *L. mutus* a *L. articus* a mediados de junio, y el segundo a aves paserinas a fines de junio. Los individuos monitoreados con cámaras de video consumieron 94–110 kg de alimento por nido durante el período con polluelos, una cantidad mayor a la estimada previamente. La utilización combinada de registros de cámaras de video, restos de presas y egagrópilas fue importante para documentar la dieta de *F. rusticolus* con precisión, y recomendamos fuertemente utilizar cámaras de video con registros intermitentes en estudios futuros sobre la dieta para poder identificar los sesgos en los datos obtenidos a partir de restos de presas y egagrópilas.

INTRODUCTION

The Gyrfalcon (*Falco rusticolus*) is the largest of all falcons and nests primarily north of 60°N latitude across the Northern Hemisphere. It preys on vertebrates weighing from 5 to 4500 g (Clum and Cade 1994, Cade et al. 1998). Overall, the species relies on ptarmigan (*Lagopus* spp.) for much of its food, but differences among regions exist (Clum and Cade 1994). Gyrfalcons have been studied in Alaska (Cade 1960, Roseneau 1972, Bente 1981), Canada (Muir and Bird 1984, Poole and Boag 1988, Platt 1989), and in several areas across Eurasia (Kishchinskii 1957, Nielsen 1986, Huhtala et al. 1996), but the species has received little scien-

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tific attention in Greenland (Fletcher and Webby 1977, Cade et al. 1998).

Three studies briefly addressed Gyrfalcon diet in central west Greenland. Burnham and Mattox (1984) observed many passerine feathers late in the nesting period at Gyrfalcon eyries and concluded the species relies at least partially on passerines and arctic hares (*Lepus arcticus*) for prey. No collections were reported, and they did not provide quantifiable prey numbers, relative frequencies, or biomass estimates. Jenkins (1982) ranked prey species occurrence in the diet at one nest site in central west Greenland by collecting prey remains, and M. Yates and others (unpubl. data) documented prey delivered during observations of nesting Gyrfalcons. No studies have investigated this topic as a primary objective, and our current understanding of Gyrfalcon food habits in central west Greenland is limited.

Food can be a primary limiting factor for birds (Newton 1998). In their studies of Gyrfalcons in arctic Canada, Shank and Poole (1994) concluded that Gyrfalcon population size was limited by nesting locations and sufficient prey biomass. In our study area, Burnham (1975) suggested prey availability was an important factor limiting falcon density. Since 1972, more than 60 historical Gyrfalcon nest sites have been identified in central west Greenland (W. G. Mattox, unpubl. data). Most sites appeared unused in any given year, and in some years, surveyors found no breeding Gyrfalcons. Thus, nest sites do not appear to be limiting. Rather, prey abundance is likely a primary factor limiting Gyrfalcon population size and density. To investigate this theory, we must first identify the primary prey species on which Gyrfalcons depend. Therefore, the objective of this paper is to describe and quantify Gyrfalcon diet composition during the nesting period in central west Greenland.

METHODS

STUDY AREA

W. G. Mattox established the study area in central west Greenland during the Greenland Peregrine Falcon Survey (Mattox and Seegar 1988). This area (7000 km^2) extends from 66°45′N to 67°30′N latitude and 49°55′W to 52°05′W longitude and experiences continuous daylight from May to August.

The area is mountainous, treeless tundra with numerous small lakes and cliffs. The floral community is primarily short willow (*Salix* spp.), dwarf birch (*Betula nana*), sedges (*Carex* spp.), and grasses. The area supports a simple fauna (Burnham and Mattox 1984) including the arctic fox (*Alopex lagopus*), arctic hare, Greenland caribou (*Rangifer tarandus*), and musk ox (*Ovibos moschatus*). No rodents occur in the area. Thirty bird species have been documented, of which 18 are observed regularly (Burnham and Mattox 1984, Meese and Fuller 1987). Gyrfalcons, Peregrine Falcons (*Falco peregrinus*), White-tailed Sea Eagles (*Haliaeetus albicilla*), and Common Ravens (*Corvus corax*) are the avian predators in the study area. Four passerine species, besides the raven, occur in our study area, including Lapland Longspurs (*Calcarius lapponicus*), Snow Buntings (*Plectrophenax nivalis*), Common Redpolls (*Carduelis flammea*), and Northern Wheatears (*Oenanthe oenanthe*). Other potential Gyrfalcon prey include Rock Ptarmigan (*Lagopus mutus*), Mallard (*Anas platyrhynchos*), Long-tailed Duck (*Clangula hyemalis*), Red-breasted Merganser (*Mergus serrator*), Common Ringed Plover (*Charadrius hiaticula*), Purple Sandpiper (*Calidris maritima*), Red-necked Phalarope (*Phalaropus lobatus*), Glaucous Gull (*Larus hyperboreus*), and Iceland Gull (*Larus glaucoides*). We conducted research in the study area from April to August in 2000 and 2001. For a more detailed description of the study area, see Burnham and Mattox (1984).

VIDEO IDENTIFICATION OF PREY

We surveyed historical Gyrfalcon nest cliffs in April and May of each year by foot, helicopter, and fixed-wing aircraft. We selected occupied nests for videosurveillance based on proximity to a second occupied nest. This allowed us to monitor two nests concurrently from a single base camp. We used nest numbers (1–4, assigned alphabetically by cliff name) instead of actual cliff names to protect nest locations.

We installed solar-powered, time-lapse Sentinel All-Weather Video Surveillance Systems (Sandpiper Technologies Inc., Manteca, California) at four nests to record prey deliveries to eyries (Booms and Fuller, in press). We mounted the small videocameras within 1 m of the eyries and connected cameras to separate recording units. The units recorded 20 frames sec^{-1}, allowing 24-hr recordings on one 8-hr videotape. As logistics allowed, we changed tapes daily to maintain continual video coverage.

In 2001, we began recording at nests 1 and 4 halfway through incubation (mid-May). Both nests were located in the center of the study area, approximately 40 km apart. The adult female at nest 4 was injured during the incubation period (unknown cause) and the nest failed two days after young hatched (young rolled off sloping nest ledge). We excluded data from this nest in all analyses. We began recording at nests 2 and 3 in late May 2000, when young were five and seven days old respectively. Both nests were located in the northeast corner of the study area, approximately 25 km apart. We stopped filming after young fledged (approximately 50 days old). Nests 1, 2, and 3 fledged four, two, and three young, respectively. We used video only from the nestling period in this study. Nests 1, 2, and 3 were located approximately 120, 130, and 140 km from the Greenland coast, respectively.

We recorded 2677 hr of videotape from the three nests covering an average of 77% of the nestling period (nest 1: 94%, nest 2: 87%, and nest 3: 49%). We recorded fewer hours at nest 3 because overland distance between it and base camp prevented daily tape changes until travel by boat was possible. Therefore, we recorded 8 hr per day until young were approximately 26 days old, after which we recorded 24 hr per day. Other than these missed hours, interruptions in coverage at the three nests were minimal, were distributed fairly evenly across the nestling period, and were typically results of brief mechanical failure.

We summed the number of whole or headless items delivered to each nest and identified each item to the lowest taxonomic level possible. We were unable to identify some small birds that were either passerines or shorebird young, and we placed these items in a generic small bird category. We tallied individual parts of dismembered prey delivered within approximately 24 hr of each other until they represented one individual. Adult Gyrfalcons sometimes remove uneaten portions of prey from the nest and cache these items for future consumption (Cade et al. 1998). To minimize double counts of cached prey, we recorded the condition of prey upon delivery and removal (if removed). If a delivered item looked like one recently removed from the nest, we considered the item retrieved from a cache and did not record it as a new item.

After determining the minimum number of individuals present in video, we multiplied those numbers by the average prey category biomass (Table 1) to estimate total biomass consumed and the relative proportion that each species or category contributed to the diet (Poole and Boag 1988). We counted adult females as one ‘‘nestling’’ when estimating biomass delivered per nestling (i.e., we divided by brood size + 1; Poole and Boag 1988) because the adult females often fed themselves while feeding young.

PREY REMAINS AND PELLETS

We collected prey remains and pellets from the eyrie, below the eyrie, and accessible perches of occupied nest cliffs in 2000 and 2001 from across the study area. We discarded items that were noticeably weathered, which we presumed were from previous years. Upon installing cameras at video-monitored nests, we removed and excluded from analysis all pellets and remains from the above locations to eliminate material deposited before the nestling period. Hence, remains and pellets collected from video-monitored sites reflect only diet from the nestling period and are directly comparable to video data.

We collected prey remains and pellets from 14 non-video-monitored nest cliffs twice in each field season (Hunter et al. 1988, Huhtala et al. 1996, Nielsen 1999). We first collected items when nestlings were approximately 18–28 days old (roughly mid-June) and made the second collection after young fledged (roughly mid-July). We also collected remains and pellets from five additional nests only during the first collection and from three additional nests only during the second collection (total 22 nests). Because we did not visit non-video-monitored nests before the nestling period, collections included material from the prenesting, incubation, and nestling periods. Therefore, we do not make direct comparisons between video observations and prey remains or pellets collected from non-video-monitored nests.

We identified the minimum number of individuals present in prey remains based on the most commonly found bone or body part representing one individual (Poole and Boag 1988, Nielsen 1999). This was the sternum for Rock Ptarmigan, hind legs for arctic hares, and wings for passerines. Based on video observations, Gyrfalcons often consumed passerines whole. We recorded the presence/absence of flight feathers if no passerine body parts were found. This likely underestimated the number of passerines consumed, although we do not know to what extent.

F. Doyle analyzed the pellets according to Errington (1932), Marti (1987), and Doyle (2000). Each pellet was dissected and contents identified using reference keys by Chandler (1916), Day (1966), Adorjan and Kolenosky (1969), Moore et al. (1974), and field collections from our study area. Doyle estimated percent prey species composition in each pellet (Nielsen and Cade 1990). For example, if one pellet contained half arctic hare and half Rock Ptarmigan remains, the pellet scored 0.5 arctic hare and 0.5 Rock Ptarmigan. We calculated proportional diet composition for each prey category by dividing its cumulative score from all the pellets by the total number of pellets.

Young arctic hares and arctic foxes grew during the Gyrfalcon nestling period. To best estimate biomass for these prey, we matched the date displayed on the video image with published growth curves (Parker 1977, Prestrud and Nilssen 1992). We assumed Gyrfalcons began capturing young as soon as the young emerged from their den. We used the average fox pup emergent mass of 407 g and a gain of 26 g every day thereafter until young were approximately 120 days old and weighed 3000 g (Prestrud and Nilssen 1992). Arctic hare young (hereafter leverets) weigh an average of 100 g at birth, and gain 45–50 g per day for the first six weeks of life until they weigh approximately 2800 g (Parker 1977). We estimated an average birth date each year for leverets by visually approximating the mass of the first delivered leveret. From this estimated mass we subtracted 100 g (birth weight) and divided the difference by 45 g day^{-1} to arrive at an age estimate and subsequent birthdate. We assigned this birth date to all leverets delivered in that year and estimated their biomasses assuming they gained 45 g per day.

STATISTICAL ANALYSIS

We grouped small birds and passerines together to calculate Shannon-Wiener diversity indexes. We followed the $\log_2$ equation to calculate H-values based on the number of prey documented in each nest (Krebs 1978).

All data sets failed to meet the normality assumption, so we used nonparametric tests. We used Wilcoxon paired-sample tests to investigate differences in diet between the first and second prey remains and pellet collections. We used paired data from 14 nests for the analyses and conducted separate tests to identify changes in Rock Ptarmigan, arctic hare, and passerine occurrence between the two collection periods. To compensate for potentially inflated Type I error rates by making multiple comparisons, we chose a significance level of $P < 0.03$ (SAS Institute Inc. 2001).

RESULTS

VIDEO

Videomonitoring indicated that passerines and small birds collectively constituted the majority of the diet by frequency, followed by ptarmigan and leverets (Table 1). However, ptarmigan and leverets combined supplied over 90% of the total biomass (Fig. 1). Passerines contributed little biomass, as did foxes and Long-tailed Ducks, which were only observed at nest 1. The Shannon-Wiener diversity index (H) for the videomonitored nests averaged 1.47.

We could not identify most passerine species delivered to nests 2 and 3. Better camera placement allowed us to identify 83% of the passerines delivered to nest 1, of which Lapland Longspur fledglings constituted 76% of 134 delivered passerines. Based on field observations and the influx of passerine prey in late June (discussed below), we expect the proportions of Lapland Longspur fledglings at nests 2 and 3 were similar to nest 1. All Rock Ptarmigan and Long-tailed Ducks were adults, and all arctic hares and arctic foxes were juveniles.

Diet composition changed twice during the nestling period (Fig. 2). The first shift occurred in mid-June, when Gyrfalcons reduced their ptarmigan intake and began consuming leverets. After mid-June, leverets contributed the majority of biomass. A second diet shift was apparent in late June, when Gyrfalcons began taking high numbers of passerines, though this shift was less noticeable in terms of biomass.

Gyrfalcons from nests 1, 2, and 3 consumed 99, 82, and 54 kg of food, respectively, while being videomonitored, and we estimate they consumed 106, 94, and 110 kg, respectively, from hatching to fledging. We estimate biomass delivered per nestling was 21, 28, and 31 kg at nests 1 (4 young + 1 adult), 3 (3 young + 1 adult), and 2 (2 young + 1 adult), respectively.

TABLE 1. Relative frequencies (mean ± SE) of prey consumed at Gyrfalcon nests in central west Greenland in 2000 and 2001. Frequencies reflect the minimum number of discrete individuals consumed. We monitored 3 nests with videocameras and collected prey remains at and around 22 other nests during the nestling period. Results between video and prey remains are not directly comparable, because video data represent only the nestling period, whereas prey remains represent the prenesting through nestling periods. We assigned a biomass value to each prey category to estimate biomass composition.

Prey	Relative frequency (%)		Assigned biomass (g)	Source
	Video	Prey remains		
Rock Ptarmigan	25 ± 6	78 ± 4	500	Schaanning 1933
Arctic hare leveret	15 ± 2	11 ± 2	variable[a]	Parker 1977
Arctic hare adult	0	trace[b]	3778	Johnsen 1953
Arctic fox pups	1 ± 0.8	1 ± 0.8	variable[a]	Prestrud and Nilssen 1992
Passerines				
Lapland Longspur	10 ± 8	2 ± 0.4	27	Rosenfield et al. 1995
Common Redpoll	0	1 ± 0.2	18	Rosenfield et al. 1995
Snow Bunting	trace[b]	1 ± 0.4	37	Rosenfield et al. 1995
Northern Wheatear	0	1 ± 0.4	30	Rosenfield et al. 1995
Unidentified passerine	28 ± 11	trace[b]	28	Rosenfield et al. 1995
Total passerine	37 ± 1	5 ± 1.0		
Small birds[c]	17 ± 7	0	28[c]	Rosenfield et al. 1995
Waterfowl				
Long-tailed Duck	trace[b]	2 ± 0.5	870	Dunning 1993
Mallard	0	2 ± 0.5	1080	Dunning 1993
Red-breasted Merganser	0	1 ± 0.7	1020	Dunning 1993
Total Waterfowl	trace[b]	5 ± 1.3		
Ruddy Turnstone	0	trace[b]	115	Dunning 1993
Peregrine Falcon	0	trace[b]	782	Dunning 1993
Unknown	5 ± 2.5	0	variable[d]	
Total items consumed	832	1035		

[a] We estimated an average birthdate for young mammals from video data and then calculated their weight for the day they were delivered using the appropriate growth curve. For prey remains, we assigned the average mass of those items documented on video (888 g for leverets, 552 g for fox pups).

[b] Trace items were those contributing <1%.

[c] Includes passerines and shorebirds when these were indistinguishable on video. We assigned these items the average mass of the four passerine species.

[d] Biomass of unknown prey items was visually estimated.

PREY REMAINS

Ptarmigan were the majority of prey items in the diet as determined from prey remains, distantly followed by leverets, passerines, and waterfowl (Table 1). The same pattern held true for biomass, with ptarmigan contributing four times more biomass than arctic hares (Fig. 1). Waterfowl replaced passerines as the third largest contributor of biomass.

Percent ptarmigan and leveret biomass between collections differed significantly, with ptarmigan declining and hares increasing (Fig. 3). No other categories shifted obviously. Ptarmigan, waterfowl, Peregrine Falcon, and Ruddy Turnstone (*Arenaria interpres*) remains were from adults. Passerine remains (typically individual primary feathers) were difficult to age unless we found portions of the wing. Of 30 collections where we assigned an age class to at least one passerine, 16 (53%) contained feathers from young of the year and 14 (47%) contained adult feathers. We found remains from one adult arctic hare, and all others were leverets. All foxes were young of the year. We computed a Shannon-Wiener *H*-value of 1.28 from prey remains.

PELLETS

Leverets contributed the most pellet material, followed closely by Rock Ptarmigan (Fig. 1). Pellet composition for Rock Ptarmigan, leverets, and passerines from the two collection periods differed significantly (Fig. 3). Ptarmigan were the primary prey in the first collection, but were replaced by leverets in the second collection. Percent passerine composition increased more

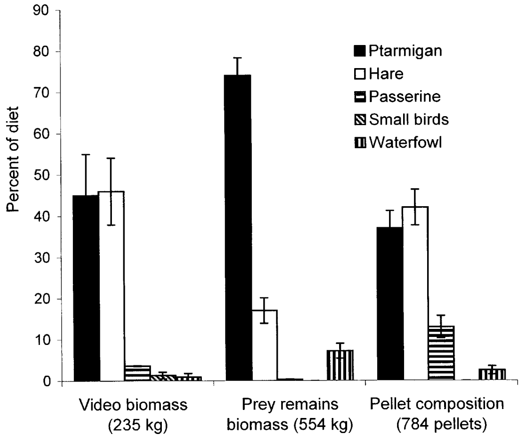

FIGURE 1. Diet composition (mean ± SE) for Gyrfalcons in central west Greenland in 2000 and 2001. Video, remains, and pellets taken from 3, 22, and 19 nests, respectively. Traces of Gyrfalcon, gull, alcid, and unidentified shorebird were found in pellets, but not included in this figure. Remains and pellets represent diet during prenesting, incubation, and nestling periods. Video represents diet during the nestling period. We used the small birds category for items that likely were passerines or young shorebirds but could not be distinguished.

than twofold from the first to the second collection.

Ptarmigan were more prevalent in pellets from perches (62%) than from the nest area (28%). Conversely, leverets were more prevalent in pellets from the nest area (47%) than from perches (17%). Passerine composition was similar: 16% from the nest area, 14% from perches.

All ptarmigan were adults, and all hares were juveniles. Fourteen percent of gull remains were from juveniles; the remaining unknown. Of the 16 passerines aged, 13 were young of the year and 3 were adults. Two pellets contained feathers and bones of juvenile Gyrfalcons. Ages of other prey from pellets were unknown.

COMPARISON OF TECHNIQUES

Video, prey remains, and pellets from the video-monitored nests provided different estimates of diet composition (Table 2). Ptarmigan and hares contributed nearly equal proportions of biomass to the diet observed on video. Conversely, in prey remains, ptarmigan biomass was more than three times greater than arctic hare biomass. Pellet data produced a twofold difference in the same direction. Passerines contributed the third most biomass from video and pellet composition data, but Long-tailed Ducks ranked third in prey remains biomass data. Prey remains and pellets detected traces of species not detected in video.

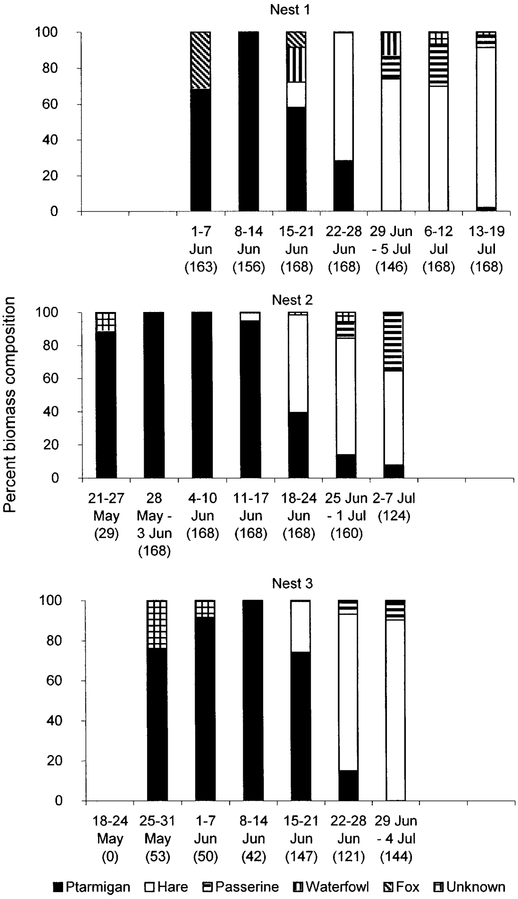

FIGURE 2. Weekly diet biomass composition for three video-monitored Gyrfalcon nests in central west Greenland during 2000 (nest 1) and 2001 (nests 2 and 3). First and last date given for each nest is the respective hatching and fledging date. The number of hours recorded per week appears in parentheses. Video recorded a total of 99, 82, and 54 kg of food delivered to nests 1–3, respectively.

DISCUSSION

METHODOLOGICAL CONSIDERATIONS

Data from Falconiformes pellets and prey remains are often biased (Snyder and Wiley 1976, Marti 1987, Rosenberg and Cooper 1990, Oro and Tella 1995, Redpath et al. 2001). Conversely, direct observation (time-lapse video in this study) can provide an essentially unbiased view of diet composition and is the most accurate as-

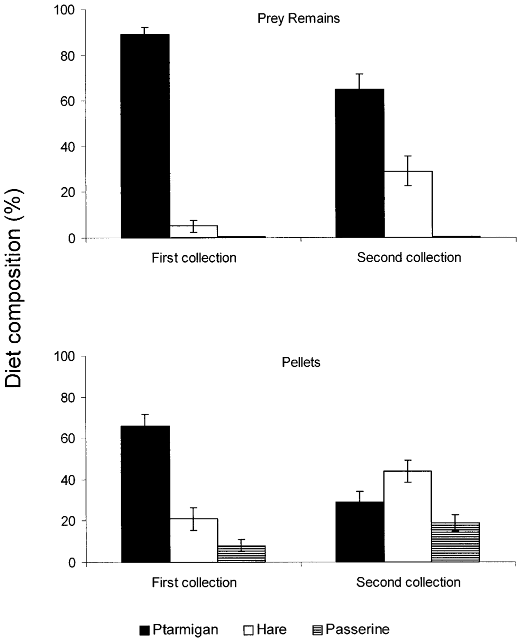

FIGURE 3. Shift in diet composition at 14 Gyrfalcon nests in central west Greenland in 2000 and 2001. Prey remains and pellets were collected twice, once when young were approximately 18–28 days old and once after young had fledged. Only prey categories contributing more than 5% of diet are shown. Wilcoxon paired-sample tests indicated a significant shift in the proportion of ptarmigan and hares in both pellets and prey remains between the two collection periods. Pellets also indicated a significant shift in the proportion of passerines in the diet (all $T_{13} \geq 2.7$; all $P \leq 0.02$). Results are based on 274 kg of prey remains and 231 pellets from the first collection and 241 kg of remains and 391 pellets from the second collection.

sessment of diet (Marti 1987). Therefore, we assume our video data closely approximate the true diet, at least at the continuously monitored nests 1 and 2. Estimates from nest 3 may be biased toward leverets, as we recorded fewer hours during the first half of the nestling period, when ptarmigan were the primary prey.

Prey remains and pellets from non-video-monitored nests may have overestimated ptarmigan occurrence in the diet for two reasons. First, we were unable to make a second collection at five of the 22 nests, missing the period when leverets were the Gyrfalcon's primary prey. Second, prey remains and pellets from non-video-monitored nests included material from prenesting and incubation periods when Gyrfalcons probably relied heavily on Rock Ptarmigan. Video data characterized only nestling-period diet.

Comparisons among techniques at the video-monitored nests revealed that prey remains and pellets were highly biased. We speculate ptarmigan were overrepresented in prey remains because Gyrfalcons rarely consume sternums (Langvatn 1977). In contrast, video showed that Gyrfalcons completely consumed small leverets, leaving remains only from large leverets (1000 g or more) to be counted. Gyrfalcons sometimes removed remains from large leverets from the eyrie, eliminating some of these remains from collections. On video, Gyrfalcons almost always completely consumed passerines, so their underrepresentation in prey remains is unsurprising.

TABLE 2. Relative diet composition (mean ± SE) at three Gyrfalcon nests as estimated using video, prey remains, and pellet analysis in central west Greenland in 2000 and 2001. Data from the three methods represent diet during the same period and are directly comparable. We considered video data, which was recorded nearly continuously, to be the most accurate method and to closely approximate true diet composition during the period of videorecording.

Prey	Video % biomass	Prey remains % biomass	Pellets % composition
Rock Ptarmigan	45 ± 10	74 ± 17	58 ± 15
Arctic hare	46 ± 8	22 ± 14	26 ± 12
Passerines	4 ± 0.1	0.2 ± 0.1	15 ± 7
Arctic fox	1 ± 1.0	0.4 ± 0.4	0
Long-tailed Duck	1 ± 1.0	3 ± 1.7	0
Mallard	0	1 ± 0.8	0
Unknown gull	0	0	0.2 ± 0.2
Unknown shorebird	0	0	0.1 ± 0.1
Small bird	1 ± 0.8	0	0
Unknown	2 ± 0.6	0	0
Totals	235 kg[a]	123 kg[a]	147 pellets[b]

[a] Estimated total biomass of prey delivered while video was recorded.

[b] Actual number of pellets analyzed.

Ptarmigan were overestimated in pellet data possibly because feathers might be more obvious in pellets than gray leveret fur (Simmons et al. 1991), and feathers and fur might have different digestibility (Rosenberg and Cooper 1990). Also, ptarmigan probably have higher surface to volume ratios than most leverets, and likely contribute proportionally more to pellet material. We propose the same explanation for passerines overestimated in pellet data, since they have the highest surface to volume ratio of prey species. Additionally, all indigestible material in passerines was ingested, unlike the larger bones of ptarmigan and some leverets, which were left as prey remains.

Video data are expensive and time intensive (Booms and Fuller, in press), but can be accurate and highly detailed. Pellets and prey remains can provide data from a larger sample and contribute to a more complete description of species in the diet, but often bias estimates of diet, as demonstrated in this study. We strongly suggest using all three methods to obtain the most comprehensive and least biased picture of Gyrfalcon diet, with video from a subsample of nests used to describe and quantify biases in prey remains and pellets.

TEMPORAL DIFFERENCES IN DIET

Results from all three data sources revealed seasonal diet shifts, but video and pellets revealed a second diet shift missed by prey remains. Other researchers have found similar shifts, with ptarmigan as the primary prey early, but replaced by alternative prey species such as waterfowl, shorebirds, or arctic ground squirrels (*Spermophilus parryii*) in Iceland and Canada (Poole and Boag 1988, Nielsen and Cade 1990, Clum and Cade 1994).

The first diet shift corresponded with Rock Ptarmigan molting into cryptic plumage and a decline in males displaying atop rocks. Concurrently, leverets emerged from their nests. The timing of the diet shift suggests a behavioral response by Gyrfalcons to decreasing ptarmigan availability and to a new source of vulnerable leverets. Poole and Boag (1988) noted a similar response to juvenile arctic ground squirrels. The second diet shift, in late June, coincided with the appearance of passerine nestlings and fledglings on the landscape, which also suggests a behavioral response to a new source of young, vulnerable prey.

GENERAL DIET

Gyrfalcons in our study area in 2000 and 2001 relied heavily on Rock Ptarmigan and arctic hare leverets as their primary prey. Few other studies have found hares to be a significant proportion of Gyrfalcon diet, notably on Ellesmere Island (Muir and Bird 1984) and in northeast Greenland (Fletcher and Webby 1977). Gyrfalcons in such areas may be constrained by the lack of alternative prey species, as both studies noted that few alternative prey species were present, and this was also the case in our study area. This may explain why, in some years, researchers did not find breeding Gyrfalcons in our study area (W. G. Mattox, unpubl. data), and underscores the importance of arctic hares to Gyrfalcon populations in areas where few alternative prey exist.

Previous investigators in our study area have suggested Gyrfalcons were at least partially dependent on passerines, waterfowl, and arctic hares (Jenkins 1982, Burnham and Mattox 1984). We found these species in the diet, but neither passerines nor waterfowl contributed significantly to total diet biomass. Other studies may have been conducted at low points in the ptarmigan's population cycle (Holder and Montgomerie 1993), leading researchers to conclude that passerines and waterfowl were more important than we observed. Additionally, previous studies in central west Greenland were based on either small sample sizes or subjective estimates.

Foxes have been documented in Gyrfalcon diets, but the authors dismissed them as carrion rather than prey (Hagen 1952, Langvatn and Moksnes 1979). The seven fox pups recorded at nest 3 on video appeared freshly killed, with limp bodies and flowing blood. The pups were similar to leverets in size, color, and overall shape, so we see no reason why Gyrfalcons would not prey on fox pups.

Previous food-intake estimates of nesting Gyrfalcons were based on standard metabolic equations (Cade et al. 1998) or prey remains (Cade 1960, Bengtson 1971, Poole and Boag 1988). Cade et al. (1998) estimated that an adult pair with four nestlings would consume 77.1 kg of food from egg laying until fledging. Poole and Boag (1988) documented 22–85 kg of food consumed during the same period from prey remains. Bengtson (1971) estimated that two adults and four young consumed 88 kg of food during the incubation and nestling periods.

Since video provided almost continuous coverage at nests 1 and 2, our estimates covering the nestling period at these nests should be close to actual amounts consumed, even though they are higher than any previous estimate covering the entire nesting period. Our results are higher because (1) prey remains analysis likely missed some items completely consumed or removed; (2) standard metabolic equations may not accurately estimate real situations; and (3) variation exists among nests, individual birds, and study areas. We therefore suggest that nesting Gyrfalcons consume more food than previously thought.

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