Ornis Fennica 73:78–87. 1996

Food niche of the Gyrfalcon *Falco rusticolus* nesting in the far north of Finland as compared with other choices of the species

Kauko Huhtala, Erkki Pulliainen, Päivi Jussila & Paavo S. Tunkkari

Huhtala, K., Department of Zoology, University of Oulu, Linnanmaa, FIN-90570 Oulu, Finland
Pulliainen, E., Department of Zoology, University of Oulu, and Värriö Subarctic Research Station, University of Helsinki, Linnanmaa, FIN-90570 Oulu, Finland
Jussila, P., Tunkkari, P. S., Värriö Subarctic Research Station, University of Helsinki, Linnanmaa, FIN-90570 Oulu, Finland

Received 5 September 1995, accepted 1 March 1996

Food habits of the Gyrfalcon *Falco rusticolus* were studied in Finnish Forest Lapland by analyzing remnants of prey and pellets from six eyries. Birds made up 98–100% of the total prey biomass identified. Ptarmigan (Willow Grouse *Lagopus lagopus* and Rock Ptarmigan *Lagopus mutus)* were the main prey items, constituting 63–86% of the total biomass. In the main study area, SE Forest Lapland, the proportion of ptarmigan in the diet over six years was lower (49–71%) and the diversity higher (H'=0.49–0.65, H'_{max}=0.90) than in Central or W Forest Lapland. Large-sized tetraonids and waders were the main alternative prey in SE Forest Lapland, constituting 10–20% and 6–24% of the total biomass, respectively. The Gyrfalcon, a ptarmigan specialist, showed flexibility by responding to high densities of new prey items, e.g. microtines and by switching to preying on waders, especially the very conspicuous and adequate-sized Whimbrel *Numenius phaeopus*, when the vulnerability of the Willow Grouse decreased, although that species was still the preferred prey.

1. Introduction

The Gyrfalcon *Falco rusticolus* is a circumpolar falconid which represents a continuum of mobility patterns from a more or less resident mode of life to nomadic or regular migratory ones (see the review by Cramp et al. 1980). Previous studies of the nutrition of both nestlings and adults during the breeding season (see e.g. Cade 1960, Bengtson 1971, Cramp et al. 1980, Poole & Boag 1988, Nielsen & Cade 1990) have shown that they consume a wide spectrum of prey animals, from birds (tetraonids, especially ptarmigan, also waterfowl, alcids, waders, owls, passerines, etc.) to mammals (lagomorphs, microtines, etc.), although certain very strong preferences can be recognized in their choices.

The Gyrfalcon is very rare in Finland, the number of breeding pairs being approximately 30 (Koskimies 1989). The present authors have studied its feeding biology in Finnish Forest Lapland, paying special attention to the breadth of the food niche from the standpoint of the nesting of this arctic species in "extreme southerly" conditions. The feeding habits of the species have been studied earlier by Mikkola & Sulkava (1972) in Finnish Fjeld Lapland and by Pulliainen (1975a) in Finnish Forest Lapland. The aim of this paper is to compare the food niche characteristics of the Gyrfalcon breed-

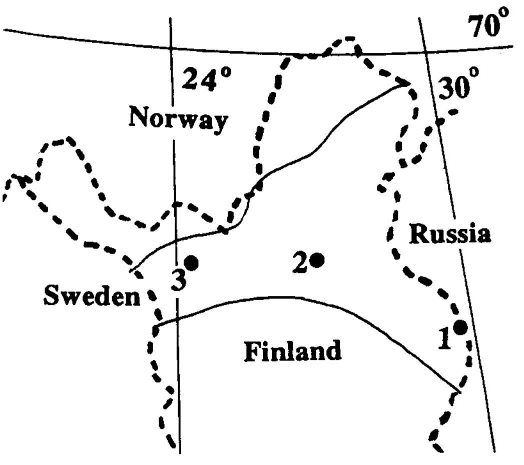

Fig. 1. Study areas: 1. Salla, 2. Inari, 3. Enontekiö. The borders of Forest Lapland according to Kalliola (1973).

ing in Finnish Lapland with the corresponding data available for other breeding territories.

2. Material and methods

The study was mainly conducted in the district of Salla, SE Finnish Forest Lapland (Fig. 1). The major part of the area consists of lowland forests (70%) with Norway Spruce *Picea abies,* Scotch Pine *Pinus sylvestris* and Birch *Betula spp.* as the main tree species. Subalpine birch forest accounts for 7% of the area, bogs for 13% and alpine fell summits for 1%.

The climate of Salla is continental, with relatively warm summers and cold winters. July is the warmest month and January the coldest, the mean temperature for these months between 1961 and 1990 being 13.9°C and–14.5°C, respectively. There is still snow on the ground at the time when the Gyrfalcon commences egg laying in early April.

Only one pair of Gyrfalcon has been observed to breed annually in the area, breeding having been first observed at the site in 1973 (Pulliainen et al. 1973, Pulliainen 1975a) and later in 1974, 1985, 1988, 1989, 1990 and 1991. The nesting site was very similar to those described by Langvatn & Moksnes (1979) in central Norway. The eyrie was situated in the subalpine zone (420 m above sea level) at a distance of 300 m from the alpine zone. It was on a south-facing ledge on the north wall of an east-west oriented ravine, 12 m above the foot of the steep wall and 5–6 m below its top. The ledge was partly sheltered at the top and the sides. In the bottom of the ravine there was a creek running below old spruces, but there were only birches in the immediate vicinity of the nesting ledge. In 1991 the eyrie was on the same wall but about 50 m east of the previous site. Both eyries had originally been built by Ravens *Corvus corax.*

Remnants of prey were collected from beneath the nesting ledge and from the surroundings of the eyrie during breeding. In 1989 remains were collected from the eyrie on 8 June when the young were about three weeks old, while in the other years collection from the eyrie took place only after the young had already fledged. The majority of the remnants were skeletons or individual bones, the rest consisting of pluckings and pellets (N=112). Items obviously aged were counted separately and pellets of uncertain origin were discarded. The prey remains were identified with the aid of the reference collection in the Zoological Museum of Oulu University. The two *Lagopus* species, the Willow Grouse and the Rock Ptarmigan, could not be differentiate apart by skeletal fragments. The minimum number of individuals was determined by combining skeletal fragments and other body parts into probable units with regard to species, size and age, as described by Langvatn (1977).

Additional material was collected in the districts of Inari and Enontekiö, central and W Finnish Forest Lapland, respectively (Fig. 1). Remnants of prey and pellets were collected once a year from two eyries in Inari, one in 1976 containing old material (no pellets) and the other in 1986 containing both fresh and old remains of prey and 12 pellets. Two collections (two eyries) were made also in Enontekiö, in 1975 (no pellets) and 1976 (fresh material, containing 3 pellets).

The results are given as percentages of the total individuals identified and of the total biomass. The average weights of the prey species were used for the biomass calculations, bird weights according to von Haartman et al. (1963–1972) and mammal weights according to Siivonen & Sulkava (1994). Annual differences in diet were tested using G^2-test. Spearman rank correlation was used to examine the correlations between the density of the main prey (ptarmican) and both the diversity of the diet and the proportion of secondary prey in the diet (waders).

Similarly, the comparisons between the proportion of ptarmigan in the diet and the availability of these species was made by using the Spearman rank correlation. Shannon-Weaver diversity indices were calculated and the differences between these were tested according to Zar (1984). Eight main food categories were used to calculate the diversity of the diet: ptarmigan, other tetraonids, waterfowl, waders, other "large"-sized birds (> 120 g), other "small"-sized birds (< 120 g), "large"-sized mammals (>100 g) and "small"-sized mammals (<100 g). The categories are based more on the habitat and mode of life of the species than on taxonomy.

The statistics of the Finnish Game Research Institute, based on line-transects in 1985–1989 and on wildlife triangles in 1989–1991, were used to estimate the abundance of the tetraonids in the study area (for methods, see Lindén et al. 1989). The density of tetraonids during the nesting period of the Gyrfalcon was described using the census data for August of the same year. The results are given for the district of Salla and the neighbouring district of Savukoski, and their relevance to this particular area may not necessarily be the best possible. The densities of waders were determined by the line transect method (see Pulliainen & Saari 1993) and may be biased because of the small number of transects drawn across the alpine heath. The relative abundance of microtines was estimated by pitfall trapping.

3. Results

The Willow Grouse is the most abundant tetraonid species in the study area in Salla, its populations fluctuating widely from year to year. It is more or less sedentary in Finnish Lapland (Pulliainen 1975b) and is thus present when the Gyrfalcons start nesting in April. The densities of Willow Grouse in Salla in 1985–1991 are shown in Fig. 2. Fluctuations in the populations of the Capercaillie *Tetrao urogallus* and the Black Grouse *Tetrao tetrix* were synchronous with that of the Willow Grouse. The Rock Ptarmigan *Lagopus mutus* occurs only occasionally in this area. The Wood Sandpiper *Tringa glareola* is the most numerous wader in the area, the mean number of pairs in 1985-1993 being 3.06/km^2 and the Golden Plover *Pluvialis apricaria* (1.48/km^2), Common Snipe *Gallinago gallinago* (1.16/km^2), Whimbrel

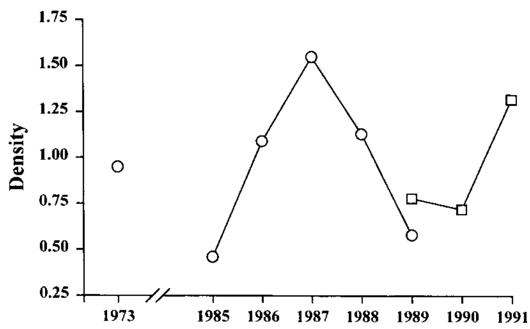

Fig. 2. Densities (individ./km^2) of the Willow Grouse in Salla/Savukoski. Circles indicate densities based on line-transects, squares wildlife triangles.

Numenius phaeopus (0.52/km^2) and Ruff *Philomachus pugnax* (0.47/km^2) are also present. The waterfowl density in the area is very low.

A cyclic low in small rodent density was recorded in 1985, after which populations increased in the following two years and reached their peak in 1988 (Kemppainen 1990, unpubl.). In 1990 the populations crashed, and they were also low in 1991. The density of the Mountain Hare *Lepus timidus* is low.

Birds were clearly dominant among the prey (Fig. 3), their estimated biomass being 96.1–99.6% of the total biomass consumed in different years. Ptarmigan was the main food item, constituting 46.8–66.2% of the prey remnants and 48.8–71.3% of the total biomass. There was no correlation between the proportion of ptarmigan in the diet and the density of the *Lagopus* species (r_s=0.0, n=4). Waders, especially the Whimbrel and Golden Plover, also occurred frequently in the diet. Altogether 28 bird species were identified. Mammals accounted for 2.9–21.3% of the prey items but only 0.4–4.1% of the total biomass. Most of the mammalian prey remnants in Salla represented microtines but young hares accounted for a greater part by biomass (Table 1).

The pellet material provided 7.4% (37 items) of a total of 499 items identified. All the microtines, the Common Shrew *Sorex araneus*, the Weasel *Mustela nivalis*, the Reindeer *Rangifer tarandus tarandus*, the Siberian Jay *Perisoreus infaustus*, an egg, the Common Frog *Rana temporaria* and *Carabus glabratus* (*Coleoptera, Carabidae*) were prey items found solely in the pellets.

Table 1. Prey selection (weight, N, % by number (N) and biomass (B)) of Gyrfalcons in Salla, Enontekiö and Inari based on collections of food remains and pellets.

		Salla			Enontekiö			Inari		
Species	Weight (g)	N	N%	B%	N	N%	B%	N	N%	B%
Tetrao urogallus female	1980	12	2,4	9,6				2	1,2	4,4
Tetrao tetrix male	1260	11	2,2	5,6						
Tetrao tetrix female	950	4	0,8	1,5				1	0,6	1,1
Lagopus lagopus/L. mutus	600	260	52,1	63,0	54	78,3	85,8	130	80,7	86,4
Tetraonidae sp. juv.	300							1	0,6	0,3
Anas penelope	700	1	0,2	0,3	2	2,9	3,7			
Anas crecca	300	3	0,6	0,4	1	1,4	0,8	4	2,5	1,3
Aythya fuligula	750	1	0,2	0,3	1	1,4	2,0	2	1,2	1,7
Mergus serrator	1000				1	1,4	2,6			
Bucephala clangula	750	1	0,2	0,3						
Eudromias morinellus	120	1	0,2	0,05						
Pluvialis apricaria	180	30	6,0	2,2				2	1,2	0,4
Gallinago gallinago	100	3	0,6	0,1						
Scolopax rusticola	300	4	0,8	0,5				1	0,6	0,3
Numenius phaeopus	370	64	12,8	9,6				4	2,5	1,6
Numenius phaeopus juv.	250	2	0,4	0,2						
Tringa erythropus	140	1	0,2	0,1						
Tringa glareola	60	4	0,8	0,1						
Philomachus pugnax	160	4	0,8	0,3	2	2,9	0,8	2	1,2	0,4
Scolopacidae	60	2	0,4	0,05				2	1,2	0,1
Scolopacidae juv.	50	2	0,4	0,04						
Charadriidae/Scolopacidae juv.	60	1	0,2	0,02						
Larus marinus juv.	1200	1	0,2	0,5						
Falco rusticolus pull.	300	2	0,4	0,2						
Asio flammeus	320	6	1,2	0,8						
Asio flammeus juv.	250	1	0,2	0,1						
Surnia ulula	300	6	1,2	0,7						
Corvus corone	500	4	0,8	0,8	2	2,9	2,6	3	1,9	1,7
Perisoreus infaustus	80	3	0,6	0,1						
Turdus viscivorus	120	1	0,2	0,05						
Turdus viscivorus juv.	80	3	0,6	0,1						
Turdus pilaris	110	3	0,6	0,1						
Turdus pilaris juv.	80	1	0,2	0,03						
Turdus iliacus	60	8	1,6	0,2				2	1,2	0,1
Turdus sp. juv.	40	3	0,6	0,05				1	0,6	0,04
Pinicola enucleator	50	1	0,2	0,02						
Fringilla montifringilla	20	1	0,2	0,01						
Luscinia svecica	20	1	0,2	0,01						
Anthus spp.	20	2	0,4	0,02						
Passeriformes sp.	20	1	0,2	0,01						
Passeriformes sp. juv.	15	1	0,2	0,01						
Birds total		**460**	**92,2**	**97,9**	**63**	**91,3**	**98,4**	**157**	**97,5**	**99,9**
Myopus schisticolor	25							1	0,6	0,03
Lemmus lemmus	65	5	1,0	0,1						
Microtus agrestis	35	3	0,6	0,04						
Microtus sp.	40	6	1,2	0,1	1	1,4	0,1	1	0,6	0,04
Clethrionomys rufocanus	35	7	1,4	0,1	2	2,9	0,2			
Clethrionomys glareolus/rutilus	25	1	0,2	0,01				1	0,6	0,03
Clethrionomys sp.	30				2	2,9	0,2			
Microtidae sp.	35	2	0,4	0,03						
Sorex araneus	10	2	0,4	0,01						
Mustela nivalis	45	2	0,4	0,04						
Lepus timidus juv.	500	8	1,6	1,6	1	1,4	1,3			
Mammals total		**36**	**7,2**	**2,1**	**6**	**8,7**	**1,6**	**3**	**1,9**	**0,1**
Rana temporaria	40	1	0,2	0,02				1	0,6	0,04
Egg (Turdus viscivorus)	8	1	0,2	0,003						
Carabus glabratus	1	1	0,2	0,0004						
Miscellaneous total		**3**	**0,6**	**0,02**				**1**	**0,6**	**0,04**
TOTAL		**499**	**100,0**	**100,0**	**69**	**100,0**	**100,0**	**161**	**100,0**	**100,0**

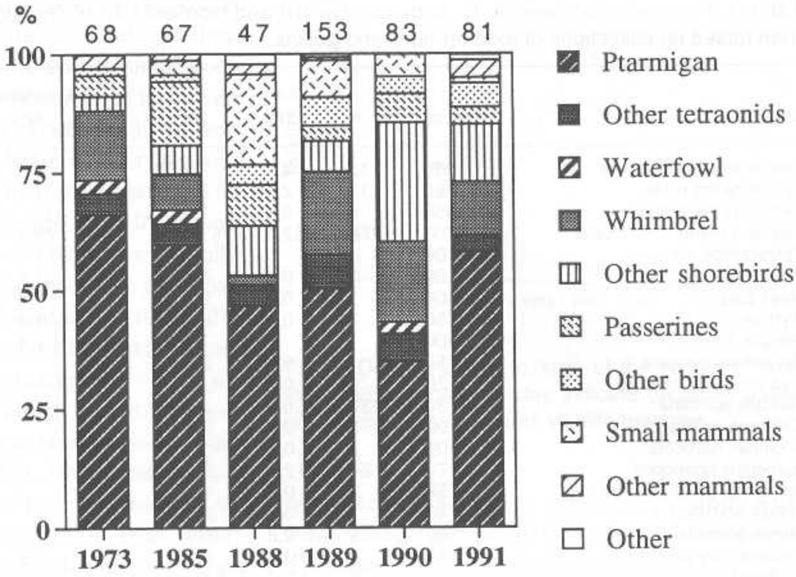

Fig. 3. Prey selection (% by number) of Gyrfalcons in Salla, based on collections of food remains and pellets. Annual sample sizes above the columns.

The diminished proportion of ptarmigan in the diet of the Gyrfalcon in the course of the breeding season in 1989 was compensated for mainly by a greater number of waders. The changes in the composition of the food brought to the eyrie during breeding are shown in Fig. 4.

There was no correlation between the density of the main prey (Willow Grouse) and the diversity of the diet in 1973 or 1985–1989 (r_s=0.40, p> 0.10) or between the density of the main prey and the proportion of the secondary prey (waders) in the diet (r_s=–0.40, p> 0.10).

Remnants of prey collected from Inari and Enontekiö consisted of a total of 230 prey individuals identified (Table 1). The diet of the Gyrfalcon differed between Salla and Inari (X^2=54.75, df=6, p<0.0001) and between Salla and Enontekiö (X^2=36.66, df=5, p<0.0001), but not between Inari and Enontekiö (X^2=7.63, df=3, p>0.05). Although year to year differences existed in the composition of the diet in Salla (G^2=63.081, df=20, p<0.0001), the data were combined to examine general food habits.

The diversity indices for the six years in Salla were 0.49, 0.57, 0.65, 0.61, 0.63 and 0.53 respectively (H'_{max}= 0.90), the differences between those for 1973/1988 (p<0.05) and 1973/1990 (p<0.05) being significant. Diversity indices (eight food categories) calculated from 12 sets of data published earlier for different parts of the breeding territories of the Gyrfalcon are shown in Table 2.

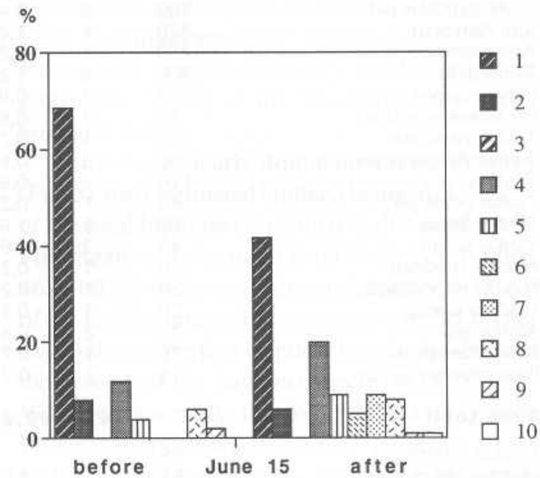

Fig. 4. Changes in the proportions of prey items (% by number) during breeding by the Gyrfalcon in Salla in 1989. Legends: 1. Ptarmigan, 2. Other tetraonids, 3. Waterfowl, 4. Whimbrel, 5. Other shorebirds, 6. Passerines, 7. Other birds, 8. Small mammals, 9. Other mammals, 10. Other.

The breeding success of the Gyrfalcon in Salla is shown in Table 3. The Gyrfalcon can achieve a high level of reproduction (Table 3) even in situations where there is quite a low density of the Willow Grouse (the years 1985 and 1990, see Fig. 2).

4. Discussion

Certain points must be taken into account when evaluating the reliability of the results obtained. The two collections of prey remnants from the eyrie in 1989 resulted in a greater amount of total remains than in the years when only one collection was made after breeding. This can be explained as an indication that the parents carry some remains away from the eyrie, as discussed by Wayre & Jolly (1958), Cade (1960), Bengtson (1971) and Langvatn (1977). As Hagen (1952) and Mikkola & Sulkava (1972) point out, false proportions can easily be deduced for the larger avian and smaller mammalian prey if only remnants are considered, and it is therefore absolutely essential to analyse thoroughly all the pellets that can be found. In the present case 11 prey species were identified in the pellets only, and these additional items made up 7.4% of the total prey items. As discussed by Langvatn (1977), the number of pellets found is undoubtedly only a minor fraction of the pellets produced by the parent birds and the young during the breeding season, thus resulting in an underestimation of small (mammalian) prey. On the other hand, pellets often contain small bone fragments and feathers of *Lagopus spp.* which cannot be identified to individual, and some of these fragments may represent individuals not represented in other remnants. This can contribute to an underestimation of *Lagopus* species, as noted by Langvatn (1977), who also agreed with the suggestion of Hagen (1952) that pellet analysis on its own gives results which approach most closely the actual qualitative composition of the Gyrfalcon's diet. Hagen (1952) and Langvatn (1977) stated that different types of prey remnant should be examined in order to build up a correct picture of Gyrfalcon's feeding. Methodological differences may therefore be of great importance and should be taken into consideration when comparing studies.

Dementiev (1951) divided Gyrfalcons into two groups with respect to their feeding habits (see also Cade 1960). Either the Willow Grouse or the Rock Ptarmigan is the primary prey in inland regions (e.g. Hagen 1952, Kistehinski 1958, Cade 1960, Haftorn 1971, Mikkola & Sulkava 1972, Pulliainen 1975a, Langvatn & Moksnes 1979, Lindberg 1983, Poole & Boag 1988, Nielsen & Cade 1990, Semenov-Tjan-Shanskij & Giljazov 1991), whereas seabirds, i.e. alcids, larids and anatids, dominate the diet in coastal and insular regions (Dementiev & Gortchakovskaya 1945, Salomonsen 1951). In addition, mammals can be the primary prey. The main diet of the Gyrfalcon on Ellesmere Island consists of the Arctic Hare *Lepus arcticus* and the Collared Lemming *Dicrostonyx groenlandicus* (Muir & Bird 1984), and Collared Lemmings also formed the main part of the diet in Northeast Greenland (Fletcher & Webby 1977), while the Arctic Ground Squirrel *Spermophilus undulatus* was the main prey in the Alaska Range (Cade 1960).

Table 2. Shannon-Weaver diversity indices (H') and frequencies (%) of ptarmigan in the Gyrfalcon' diet. as calculated from comparable data. References: 1. This study, Salla, 2. This study, Inari/Enontekiö, 3. Mikkola & Sulkava 1972, 4. Lindberg 1983, 5. Hagen 1952, 6. Langvatn & Moksnes 1979, 7. Haftorn 1971, 8. Bengtson 1971, 9. Semenov-Tjan-Shanskij & Giliazov 1991, 10. Kistehinski 1958, 11./12. Cade 1960, 13. Poole & Boag 1988.

	H'	%
1. Finland, Forest Lapland a	0.61	52.6
2. Finland, Forest Lapland b	0.39	80.0
3. Finland, Fjeld Lapland	0.43	72.4
4. Sweden, Norrbotten	0.39	67.7
5. Norway, Dovre	0.10	95.8
6. Central Norway	0.30	84.0
7. Norway, Finmark	0.06	94.6
8. Iceland	0.36	23.7
9. Russia, Lapland	0.68	44.4
10. Kola Peninsula	0.58	40.8
11. Alaska range	0.49	13.1
12. Alaska, arctic slope	0.43	71.1
13. Canada, NW territories	0.43	69.9

Table 3. Reproductive success of the Gyrfalcon in Salla.

Year	Eggs	Hatchlings	Fledglings
1973	4	4	3
1974	2	0	0
1985	4	4	4
1988	4	4	3
1989	3	3	2
1990	4	3	3
1991	4	3	2
Mean	3.6	3.0	2.4
S.D.	0.8	1.4	1.3

As far as the sporadic nature of breeding among Gyrfalcons in the present "southerly" territories and the list of prey species are concerned, these results support previous findings in N Finland and the Kola Peninsula (e.g. Mikkola & Sulkava 1972, Pulliainen 1975a, Semenov-Tjan-Shanskij & Giljazov 1991). The Willow Grouse appears to be the most important food item in each of these territories, all of which are characterized by a structural scarcity of Rock Ptarmigan in relation to the abundance of Willow Grouse. The choice of the prey among the Gyrfalcons differed between Salla and Inari/Enontekiö, the proportion of *Lagopus* species being higher in the latter areas, apparently indicating higher densities of ptarmigan populations or fewer alternative prey.

The role and significance of ptarmigan in the nutrition and food selection of the Gyrfalcon can be discussed at least from the standpoints of optimal foraging theory, dietary compensation possibilities and the suitability of this species as prey for both adult and young Gyrfalcons. Nielsen & Cade (1990) discuss similar approaches to some extent when referring to a resident mode of life, general vulnerability and an "optimum prey size" for Gyrfalcons.

Pulliainen (1975a) showed that the Gyrfalcon can carry prey weighing up to 1 800 g but is able to prey on considerably larger animals. Semenov-Tjan-Shanskij & Giljazov (1991) reported a case in which a Gyrfalcon was seen eating a male Capercaillie (4 000 g) which it had just killed. Also the Arctic Hare that the Gyrfalcon preys on in Ellesmere Island likewise exceeds the size that the falcon can carry. Parents were observed returning to the nest with the hind quarters of young hares, obviously flying very hard and labouring under a heavy load (Muir & Bird 1984). Muir & Bird (1984) doubted whether a Gyrfalcon could kill an adult hare weighing up to 5500 g, but Poole & Boag (1988) had evidence that even smaller male Gyrfalcons are capable of killing and transporting adult hares in pieces. On the other hand, very small prey, e.g. lemmings (Fletcher & Webby 1977, Muir & Bird 1984) or passerines (Burnham & Mattox 1984) may account for a great part of the Gyrfalcon's diet.

According to the optimal foraging theory, natural selection will favour individuals that tend to maximize their net rate of energy intake, e.g. by prefering large food objects to small ones (Schoener 1971). In practice, pressure towards the implementation of this principle is exerted by the fact that about 150 Willow Grouse (= ca. 88 kg) are needed from the beginning of May to the first week of July to raise a "normal" number of young (mean 2.3 young in Alaska) and to feed the feeders (Cade 1960, Bengtson 1971) if this prey species is the choice. As mentioned, this was the choice here in Finnish Lapland, where the Willow Grouse was the largest of the potential prey animals with sufficient numbers available. According to Poole & Boag (1988), who calculated the biomass return per unit time spent on foraging for each prey type, larger prey items are on average vastly superior to smaller ones, and they concluded that it may not have been energetically profitable for Gyrfalcons to capture smaller prey items on trips of more than 10 min duration.

Langvatn & Moksnes (1979) state that the Gyrfalcon extensively selects birds as food, especially Lagopus sp. and species of a similar size. Cade (1960) reports that a strong preference for ptarmigan was still clearly expressed even in a year when they were scarce, a phenomenon also evident in Salla. Similarly, ptarmigan, when abundant, were the preferred prey in NE Iceland and in the Lapland Nature Reserve (Russia) even in areas possessing a great number of waterfowl (Bengtson 1971, Nielsen & Cade 1990, Semenov-Tjan-Shanskij & Giliazov 1991), hence confirming the prediction of the optimal foraging theory, i.e. that the choice of a particular prey type should reflect absolute abundance of more profitable types (Pyke et al. 1977). The data from Salla do not support this prediction, possibly due to the inadequate Willow Grouse density values or to the small sample size.

The main point now is how far this favoured prey may be replaced by other prey species when ptarmigan are scarce. In Salla it was waders, especially the Whimbrel (15 and 24 % by weight), and large-sized tetraonids (20 and 19 %) that constituted the compensatory prey in 1989 and 1990 (Table 1), years of low ptarmigan population density (Fig. 2). The high peak in the density of microtine populations in 1988 clearly increased the intake of these mammals (Fig. 3), as in a similar case reported by Lindberg (1983) in Northern Sweden.

The general pattern in most areas in the arctic is for the ptarmigan to be heavily used during the early part of the nesting cycle of the Gyrfalcon (Nielsen

1986). A shift to other species may take place later on in the breeding season. Ptarmigan were e.g. replaced by waterfowl and waders in Iceland (Woodin 1980, Nielsen & Cade 1990), by juvenile squirrels in the central Canadian Arctic (Poole & Boag 1988) and by microtines and rodent-eating raptors in Northern Alaska (Cade 1960). A corresponding shift during the breeding from ptarmigan to other prey was noted in Salla in 1989 (Fig. 4), the year of a low ptarmigan population (Fig. 2).

The flexibility of the Gyrfalcon in its choice of prey concerns not only the size of the prey individuals but also seasonal and regional variation during the year. Reports of Gyrfalcon, usually young birds, hunting in inhabited areas, can also be considered evidence of flexibility (see Jenning 1972, Tommeraas 1988).

Caution is needed when comparing the diversity of the diet between regions (Table 2). Although the data are methodologically comparable, such facts as different durations of the studies may cause biases. The yearly differences in the diversity of the diet can be statistically significant as in the present data.

The diversity of the diet was clearly highest in the Lapland Nature Reserve in Russia (0.68), followed by Salla (0.61) and the Kola Peninsula (0.58). Ptarmigan were the main prey in all these regions, which represent typical Taiga forests. The other prey categories in order of importance were large-sized tetraonids and other large birds in the Lapland Nature Reserve, waders and large tetraonids in Salla and large birds and microtines on the Kola Peninsula. In the Dovre mountains and Finnmarksvidda, Norway, the Gyrfalcons preyed almost exclusively on ptarmigan, the diversity indices being 0.10 and 0.06, respectively. Data from various regions (Table 2) giving diversity indices of 0.30–0.49 comprise miscellaneous patterns of prey selection, although ptarmigan were still the main item in most cases. One common feature in those reports, as in the regions with high diversity mentioned above, was that there were only one or two notable groups of prey besides the main species.

It was a significant negative correlation ($r = -0.65$, $p < 0.02$*) between the diversity indices (see Table 2) and the frequences of ptarmigan in the Gyrfalcons diet from 13 different parts of breeding territories of the species. So the Gyrfalcon is able to utilize of several compensatory prey species showing a flexible feature in its choice of prey.

In summary, the Gyrfalcon appears to be a mixture of a food specialist whose annual cycle is geared to that of its main prey and an opportunist that frequently responds functionally to high densities of a new prey source, being able to create a temporary specialization under unaccustomed conditions.

Acknowledgements. We are most grateful to Seppo Sulkava who identified part of the material. Seppo Sulkava and Markku Orell made many suggestions for improvements of the earlier drafts of this paper. We thank Ahti Karusalmi for technical assistance. The English text was revised by Malcolm Hicks. We wish to thank also the staff of Värriö Subarctic Research Station for assistance in the field. This paper constitutes Report No. 312 of Värriö Subarctic Research Station, University of Helsinki.

Selostus: **Tunturihaukan pesimäaikaisesta ravinnosta ja ravinnon monimuotoisuudesta**

Tämän tutkimuksen aineiston pääosa on kerätty Värriön tutkimusaseman toimesta Pohjois-Sallasta, jossa kerrallaan yksi tunturihaukkapari on pesinyt vv. 1973–1974 sekä myöhemmin 1985 ja 1988–1991. Pesät sijaitsivat vanhoissa korpinpesissä jyrkässä rotkoseinämässä. Lisäksi sekä Inarista että Enontekiöltä kerättiin ravintojätökset kahdelta pesältä. Sallasta määritettiin yhteensä 499, Inarista 161 ja Enontekiöltä 69 saalisyksilöä.

Kunkin lajin tai lajiryhmän esiintyminen tunturihaukan ravinnossa määritettiin sekä esiintymisfrekvenssinä että biomassana. Ravinnon koostumusta ja monimuotoisuutta tutkittiin eri keräysalueiden ja Sallan osalta myös eri vuosien välillä. Tutkimuksen tuloksia verrattiin eri puolilta lajin levinneisyysaluetta julkaistuihin vertailukelpoisiin tunturihaukan ravinnonkäyttötutkimuksiin.

Linnut muodostivat pääosan tunturihaukan ravinnosta. Sallasta määritettiin yhteensä 28 saalislintulajia, joiden osuus ravinnossa vaihteli vuosittain 96–100% käytetystä saalisbiomassasta. Riekon ja kiirunan yhteenlaskettu osuus oli vuosittain 47–66% saalisyksilöinä ja 49–71% biomassana ilmaistuna. Riekkokantojen ei todettu vaikuttavan tunturihaukan pesimämenestykseen. Huonoina riekkovuosina tunturihaukka käytti korvaavina ravintokohteina muita metsäkanalintuja, kahlaajia sekä pikkunisäkkäitä, mikäli niitä oli runsaasti saatavilla. Riekon ja kiirunan osuus tunturihaukan ravinnossa oli suurempi Inarissa ja Enontekiöllä (n. 86% käytetystä biomassasta) kuin Sallassa (63%). Ravintolokeron leveys (ns. Shannon-Weaver diversiteetti-indeksi) taas oli suurempi Sallassa (0.61) kuin Inarissa ja Enontekiöllä (0.39).

Kirjallisuudesta eri puolilta levinneisyysaluetta kerättyjä aineistoja vertailemalla todettiin, että tunturihaukan ravinnon monimuotoisuus korreloi negatiivisesti pääravintokohteen, riekon ja/tai kiirunan käyttöosuuden kanssa. Tunturihaukka on pesimäajan ravitsemuksessaan riekko- ja kiirunaspesialisti, joka kuitenkin osoittaa suurta joustavuutta kyetessään pääravintokohteen saatavuuden vähetessä käyttämään useita korvaavia ravintokohteita. Joustavuutta kuvastaa myös Sallassakin todettu tunturihaukan osittainen siirtyminen pesimäajan kuluessa pääravintokohteesta muihin saalislajeihin. Tämä selittynee osittain ravinnon saatavillaolon muutoksista — Riekon käyttäytyminen muuttuu vähemmän näkyväksi sen siirtyessä pesimäreviirilleen ja samalla esim. kahlaajat palaavat pesimäseuduilleen.

References

Cramp, S. & Simmons, K. E. L. (eds.) 1980: Falco rusticolus Gyrfalcon. — In: Handbook of the Birds of Europe, the Middle East and North Africa, The birds of the Western Palearctic. vol. II Hawks to Bustards. Oxford University Press, Oxford.

Bengtson, S-A. 1971: Hunting methods and choice of prey of Gyrfalcons Falco rusticolus at Myvatn in Northeast Iceland. — Ibis 113: 468–476.

Burnham, W. A. & Mattox, W. G. 1984: Biology of the peregrine and gyrfalcon in Greenland. — Medd. Grønl. 14: 1–25.

Cade, T. J. 1960: Ecology of the Peregrine and Gyrfalcon populations in Alaska. — Univ. Calif. Publ. Zool. 63: 151–290.

Dementiev, G. P. (Дементиев, Г. П.) 1951: [The order of hunting birds]. — In: Birds of the Soviet Union, vol. 1. Moscow: Soviet Science (in Russian).

Dementiev, G. P. & Gortchakovskaya, N. N. 1945: On the biology of the Norwegian Gyrfalcon. — Ibis 87: 559–565.

Fletcher, D. J. & Webby, K. 1977: Observations on Gyr Falcons Falco rusticolus in North-east Greenland. — Dansk orn. Føren. Tidsskr. 71: 29–35.

von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–1972: Pohjolan linnut värikuvin. — Otava, Helsinki (in Finnish).

Haftorn, S. 1971: Norges fugler. — Univ. press., Oslo.

Hagen, Y. 1952: The gyrfalcon (Falco rusticolus L.) in Dovre, Norway. — Norske Videnskaps-Akademi. I. Mat. Naturv. Klasse 4: 1–37.

Jenning, W. 1972: Iakttagelser rörande en övervintrande jaktfalk Falco rusticolus. — Vår Fågelvärld 31: 1–8

Kalliola, R. 1973: Suomen kasvimaantiede. — WSOY, Porvoo (in Finnish).

Kemppainen, M. 1990: Pikkunisäkkäiden esiintymisestä ja biotoopinvalinnasta Värriön luonnonpuiston kuudessa eri tutkimusbiotoopissa vuosina 1983–1989. — M. Sc. thesis, University of Oulu (in Finnish).

Kistehinski, A. A. (Кистехински, А. А.) 1958: On the biology of the gyrfalcon (Falco gyrfalco gyrfalco L.) in the Kola Peninsula. — Ornithology 1: 61–75 (in Russian with English summary).

Koskimies, P. 1989: Distribution and numbers of Finnish breeding birds. — Appendix to Suomen lintuatlas. SLY:n Lintutieto Oy, Helsinki.

Langvatn, R. 1977: Characteristics and relative occurrence of remnants of prey found at nesting places of Gyrfalcon Falco rusticolus. — Ornis Scand. 8: 113–125.

Langvatn, R. & Moksnes, A. 1979: On the breeding ecology of the Gyrfalcon Falco rusticolus in Central Norway 1968-1974. — Fauna Norv. Ser. C. Cinclus 2: 27–39.

Lindberg, P. 1983: Relations between the diet of Fennoscandian Peregrines Falco peregrinus and organochlorines and mercury in their eggs and feathers, with a comparison to the gyrfalcon Falco rusticolus. — Ph.D. thesis, University of Göteborg.

Lindén, H., Wikman, M. & Helle, E. 1989: Tetraonid populations in Finland in 1988: a comparison between the route censuses and the wildlife triangles — Suomen Riista 35: 36-42 (in Finnish with English summary).

Mikkola, H. & Sulkava, S. 1972: Mitä syö tunturihaukka. — Suomen Luonto 5: 183–185 (in Finnish).

Muir, D. & Bird, D. 1984: Food of Gyrfalcons at a nest on Ellesmere Island. — Wilson Bull. 96: 464–467.

Nielsen, O. K. 1986: Population ecology of the Gyrfalcon in Iceland with comparative notes on the Merlin and the Raven. — Ph.D. thesis, Cornell Univ., Ithaca.

Nielsen, O. K. & Cade, T. J. 1990: Seasonal changes in food habits of Gyrfalcons in NE-Iceland. — Ornis Scand. 21: 202–211.

Poole, K. G. & Boag, D. A. 1988: Ecology of gyrfalcons, Falco rusticolus, in the central Canadian Arctic: diet and feeding behaviour. — Can. J. Zool. 66: 334–344.

Pulliainen, E. 1975a: Choice of prey by a pair of Gyrfalcons Falco rusticolus during the nesting period in Forest-Lapland. — Ornis Fenn. 52: 19–22.

Pulliainen, E. 1975b: Structure of two willow grouse (Lagopus lagopus) populations in Finnish Fjeld Lapland in the winters of 1972–1975. — Ann. Zool. Fenn. 12: 263–267.

Pulliainen, E., Iivanainen, J., Korhonen, K., Ovaskainen, P. & Tolonen, A. 1973: Southern nesting of the Gyrfalcon. — Lintumies 8: 30 (in Finnish with English

summary).
Pulliainen, E. & Saari, L. 1993: Breeding biology of the Whimbrel Numenius phaeopus in eastern Finnish Lapland. — Ornis Fenn. 70: 110–116.
Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. Quart. — Rev. Biol. 52: 137–154.
Salomonsen, F. 1951: Grønlands Fugle. Part 3. — Ejnar Munksgaard, København.
Schoener, T. W. 1971: Theory of feeding strategies. — Ann. Rev. Ecol. Syst. 2: 369–404.
Semenov-Tjan-Shanskij, O. I. & Giljazov, A. S. (Семенов-Тйан-Сханский, О. И. & Гилйазов, А. С.) 1991: [Birds of Lapland]. — Nauka (in Russian).
Siivonen, L. & Sulkava, S. 1994: Pohjolan nisäkkäät. — Otava, Keuruu (in Finnish).
Tømmeraas, P. J. 1988: Gyrfalcon Falco rusticolus predation on poultry and domestic animals: a review. — Dansk Orn. Føren. Tidsskr. 82: 109–116.
Wayre, P. & Jolly, G. F. 1958: Notes on the breeding of the Iceland gyr falcon. — British Birds 51: 285–290.
Woodin, N. 1980: Observations on gyrfalcons (Falco rusticolus) breeding near lake Myvatn, Iceland, 1967. — Raptor Res. 14: 97–124.
Zar, J. H. 1984: Biostatistical analysis. — Englewood Cliffs, New Jersey.