DIET OF THE GYRFALCON (*FALCO RUSTICOLUS*) IN NORTHERN FENNOSCANDIA

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ABSTRACT.—The Gyrfalcon is a circumpolar, arctic and resident raptor in Fennoscandia and is totally dependent on only one or two ptarmigan species, the Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus muta*), for food over half of the year. The diet of the Gyrfalcon has been studied in many parts of its range in earlier decades, but recently only in a few regions. There is need for current knowledge of the availability and usage of prey, and regional and temporal variation of the diet, because the populations of the two *Lagopus* species seem to have declined in some parts of the Gyrfalcon´s range. Availability of food may thus become a limiting factor for falcon populations, and it has been identified as the main threat for viability of falcon populations in the European range, together with the availability of secure nest sites. The published studies of inland populations come from alpine and tundra regions where the Rock Ptarmigan is the most important prey species. In our study area in Finnish Lapland and neighbouring regions in northern Norway and Sweden, during breeding seasons (1998 to 2010), Willow Ptarmigan was the main prey (73.6% of total *Lagopus* spp. by number). The two ptarmigan species formed 89% of the prey individuals, and this percentage varied little among regions and landscapes, or annually, despite strong cyclical fluctuations of the ptarmigan populations. The falcons feed their young almost exclusively on *Lagopus* spp. Other species of appropriate size (waders, waterfowl, etc.) were available only from late spring to late summer, and were hunted by falcons in small numbers.
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THE GYRFALCON IS CIRCUMPOLAR and among the most arctic raptor species in the world (e.g., Cade 1982, Cade et al. 1998, Ferguson-Lees and Christie 2001, Booms et al. 2008). Although Golden Eagles (*Aquila chrysaetos*), Rough-legged Buzzards (*Buteo lagopus*), and some other birds of prey may breed almost as far north as Gyrfalcons, they are not able to live throughout winter as close to the High Arctic as Gyrfalcons do.

The Gyrfalcon is unique among raptors in its specialization for food, being dependent on only one or two prey species, the Willow

Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus muta*), during most of the annual cycle (e.g., Cade et al. 1998, Nielsen 2003, Booms et al. 2008). It is even of greater importance to note for conservation and management purposes that the Gyrfalcon starts to breed in late winter when the populations of these prey species, the only ones available at that time, are at their lowest level during their annual cycle, and that young falcons are fed with the same prey species up to fledging time, as long as they remain available (e.g., Koskimies 1999, 2006a).

There is a vital need to study the diet and availability of suitable prey of the Gyrfalcon in all parts of the species' range, because the availabilities of prey and nest sites are the primary necessities of the species for reproduction and survival. In Iceland, for example, Nielsen (1999, 2003) has shown that the proportion of pairs starting to breed depends on the density of the Rock Ptarmigan. The decline of Willow Ptarmigan and Rock Ptarmigan populations have been evaluated as the most worrying threats to the Gyrfalcon in northern Europe, together with lack of secure nest sites, according to the official Gyrfalcon Action Plan of the European Union (Koskimies 1999, 2006a). The effect of climate change could not be evaluated in an adequate manner at that time. In some regions, ptarmigan densities have probably declined to a lower level than historically known, thereby potentially limiting future Gyrfalcon densities as well, in spite of active measures against other threats (Koskimies 2006a, 2006b). The crash of the Willow Ptarmigan population in Finland and other parts of northern Fennoscandia since 2007 forced some 80–90% of the Gyrfalcon pairs to give up nesting attempts (Koskimies 2011), and if continued in the coming years, it will have a significant negative effect on the ability of the Gyrfalcon population to recover from the present exceptionally low level (Koskimies and Ollila 2009). Due to their absolute dependence on *Lagopus* spp. populations and secure nests built mostly by Ravens (*Corvus corax*), as well as being affected negatively by many types of human activities, the Gyrfalcon has been classified as endangered in Finland (Rassi et al. 2010) and vulnerable in Sweden (ArtDatabanken 2010), respectively. In Norway, the Gyrfalcon is not a threatened species thanks to a considerably larger population size compared to Finland and Sweden (Kålås et al. 2010).

The diet of the Gyrfalcon has been studied in several countries in different parts of the species range (e.g., Cade et al. 1998, Nielsen 2003, Booms and Fuller 2003, Booms et al. 2008). In Europe, research on this topic has been most intensive so far in Iceland (Bengtson 1971, Nielsen and Cade 1990, Nielsen 1999, 2003), but there are important publications also from Norway (Hagen 1952, Langvatn 1977, Langvatn and Moksnes 1979), from Sweden (Lindberg 1983, Nyström et al. 2005), and from the Kola Peninsula, Russia (Dementiev and Gortchakovskaya 1945, Kishchinskiy 1958, Giljazov et al. 2008). In the New World, diet of the Gyrfalcon has been studied in Greenland (Burnham and Mattox 1984, Booms and Fuller 2003), Canada (Poole and Boag 1988) and Alaska (Cade 1960). Summaries of these and some other minor studies have been published in recent years by Cade et al. (1998) and Nielsen (2003) from the Old World, and by Booms et al. (2008) from the New World.

In Finland, only a few minor studies have been made on the diet of the Gyrfalcon so far. Pulliainen (1975) and Huhtala et al. (1996) published material from a territory in eastern Lapland where coniferous forests predominate (prey items collected from one nest site during six years). Further north, in alpine regions, Mikkola and Sulkava (1972) listed prey items from one nest, too, and Huhtala et al. (1996) from four nests. In addition, preliminary results of our ongoing study (from the years 1998–2002) were reported in 2002 (Koskimies and Sulkava 2002). The main aim of this study was to produce knowledge on the diet of the

Gyrfalcon in Finland and in the neighboring areas in northern Fennoscandia, and to monitor the yearly and regional changes of the diet. This study was part of a larger research project by PK on the ecology and conservation biology of the Gyrfalcon in northern Fennoscandia (Koskimies 2006b, 2011).

Methods

Study Area.—The study area is in northern Finland and nearby neighboring regions in northernmost Sweden and Norway (about 68–70° N and 20–30° E). In Finland, this region is called Fell-Lapland, and is relatively flat with gently sloping fell-mountains, the highest tops reaching ca. 1,000 m above sea level. The majority of the low-level country and wide valleys between fells, as well as lower fell slopes especially in eastern Lapland, are covered by barren pine-dominated forests (Scotch Pine *Pinus sylvestris*); the higher slopes there and also the lower altitudes in western and northern parts of the area have mountain birch forests (*Betula pubescens* ssp. *tortuosa*). Boggy and wet areas in most parts of the area are fairly small and bushy, with a thin turf layer compared to more extensive and wetter peat-lands farther south in Finland. There are many small- and medium-sized lakes all over the area.

Collection of Prey Remains.—Prey remains (bones, feathers, and pellets) were collected by PK and Björn Ehrnsten mostly at the nest, under the nest on the ground, and at nearby cliff ledges, especially opposite the nest (some 10–50 m away), where the main plucking posts usually occur. Most of the samples were collected in late June, usually 1–2 weeks before the young were to fledge. In several tens of nest-sites, prey remains were gathered also in late August or early September, either in the same season or 1–2 years later (especially if the site remained unoccupied and we knew which nesting attempt the remains came from). The sample sizes varied widely depending on the characteristics and accessibility of the nest ledge. In most cases, 20–40 prey individuals were identified per sample. In total, 189 samples were collected, and 5,919 prey individuals identified from about 50 nest areas.

The male Gyrfalcon eats or removes the head, most feathers, gut, and often the legs of larger prey, such as *Lagopus* spp., before bringing it to the nest site (Hagen 1952, Bengtson 1971, Langvatn 1977, Nielsen 1986, Cade et al. 1998, Booms et al. 2008). The female may continue plucking near or in the nest. Large primaries often remain on the larger prey brought to the nest, although the prey handling behavior of the adults varies from one nest site to another (Hagen 1952, Langvatn 1977). Smaller prey species (e.g., waders, thrushes) are often brought to the nest intact, where the female plucks them (feathers are found in the nest and pellets, Poole and Boag 1988, Cade et al. 1998). Some females remove part of the prey remains from the nest (e.g., Bengtson 1971, Langvatn 1977, Jenkins 1978, Booms et al. 2008).

Identification of the Prey Remains.—SS identified the collected prey remains material. The bones of the prey were indentified using reference collections (a personal collection from our previously known prey remains, and a collection of the Zoological Museum, University of Helsinki), by bone measurements, and by referring to several books on the identification of bird bones (e.g., Woelfle 1967, Erbersdobler 1968, Cohen and Serjeantson 1996). The identification of feathers was also based on collections and reference books (März 1987, later also Brown et al. 2003). The numbers of prey animals were mostly determined by counting bones, those of the left and right sides of the body separately. To be exact in counting, it was sometimes possible to use the age of remains (fresh or old), the age of prey animals (adult or young), and the individual differences in size between prey items. Prey remains found in pellets were combined with the other remains. The majority of Norwegian Lemmings (*Lemmus lemmus*) and other small mammals were found in pellets, as also found by Hagen (1952), Langvatn (1977), and Poole and Boag (1988). Old pellets brought to the nest site by Ravens or Rough-legged Buzzards were distinguished from Gyrfalcon pellets by containing mostly fur and bones of small rodents, and were omitted from the material.

Separation of the Lagopus Species.—Distinguishing between Willow Ptarmigan and Rock Ptarmigan has been considered problematic by many researchers. In some studies, these main prey species of the Gyrfalcon have not been separated at all (Hagen 1952, Langvatn 1977, Langvatn and Moksnes 1979, Huhtala et al. 1996). But Haftorn (1971), Lindberg (1983), and Nyström et al. (2005) were able to identify *Lagopus* remains to species level based on the length of the tarsometatarsus (according to Hagen 1952 and Myrberget 1977). In the material of Erbersdobler (1968), which included 72 Willow Ptarmigan and 63 Rock Ptarmigan individuals, the lengths of the tarsometatarsus and femur of the Rock Ptarmigan were always shorter than those of the Willow Ptarmigan (tarsometatarsus of Rock Ptarmigan = 30.7–35.4 mm, and of Willow Ptarmigan = 36.6–42.6 mm; and the femur of Rock Ptarmigan = 51.6–56.3 mm, and of Willow Ptarmigan = 56.5–64.5 mm). Myrberget (1977) showed with his larger sample sizes (n = 526 Willow Ptarmigan and 192 Rock Ptarmigan metatarsi), that if metatarsi between 35.0– 35.9 mm long were excluded, and those shorter than 35.0 mm were classified as Rock Ptarmigan, and those longer than 35.9 mm as Willow Ptarmigan, only 2% of both species were misidentified. We based our species recognition on this rule. According to Erbersdobler (1968), the femurs from 56.0 mm to 56.9 long were classified as *Lagopus* spp. In our study, very few femurs were of this intermediate length.

In practice, only a minority of the *Lagopus* remains can be identified to species level, because so few intact leg bones can be found at a Gyrfalcon nest site (e.g., Langvatn 1977). In our study area, the sternum was the most abundant bone in almost every sample, and that is why we counted the number of prey individuals according to the number of sterna in the same way as done by Hagen (1952), Bengtson (1971) and Langvatn (1977). To illustrate the proportion of various bones to be found at nest sites, we counted the percentages of them compared to the number of sterna calculated from our material (833 sterna) from 1988 to 2002 (the respective percentage from Norway according to Langvatn 1977 is given in parenthesis): humerus 61.6% (64.7%), pelvis 51.3% (51.4%), femur 13.3% (13.4%), tibiotarsus 8.2% (12.3%), and tarsometatarsus 5.9% (14.9%). The male probably eats or removes a good number of legs, and many of them seem to be swallowed whole at the nest by the female or larger young (parts of broken long bones and intact shorter ones are often found in pellets).

The Importance of Old Prey Remains in Diet Studies.—In many nest sites, prey remains were collected partly or totally in the next summer or autumn after breeding, and some samples were several years old when gathered. In a study of the diet of the Peregrine (*Falco peregrinus*) farther south in Finland (Sulkava 1968), it was stated that old remains gave an insufficient picture of the proportion of small prey species. It seems to us, however, that at Gyrfalcon nests the remains are well preserved and collectible by a careful researcher in a similar species-to-species proportion as fresh remains, even several years later. To check this impression, we did two comparisons between fresh and old remains.

1. In the years 1998–2002, five samples were collected about four years after the latest nesting season. In the total material of these samples (n = 223 prey), the percentage of *Lagopus* species (87.4%) was very similar to that of the total (mainly fresh) material of the same years (85.8%, n = 1,153 prey individuals). The proportion of waders (*Charadriiformes,* the second largest prey group) was 8.1% in the old material and

6.5% in the fresh one, respectively, although it should have been *vice versa* (as waders are smaller than *Lagopus* spp.). The percentage of thrushes (*Turdus* spp.) and other small passerines was smaller (0.5%) in the old material than in the fresh one (1.1%), but the total number of prey included only a few individuals. In this comparison, the materials compared were from different nests (either old or fresh).

2. For the second comparison, the materials were collected from the years 2002–2010 from the 13 nest sites where prey remains were collected both in the year of nesting, and 1–2 years later (when the nests were unoccupied, so these prey were hunted by falcons during the same season as the fresh ones). The fresh material included 799 prey individuals, and the old material 555 prey individuals, respectively. The percentage of *Lagopus* spp. was 91.2% in the fresh material, but a little smaller in the old one, i.e. 89.5%, although it should be *vice versa* if the general belief that large prey is overestimated in old material was correct. The percentages of waders were the same (3.5% and 3.6%) in both samples, and the differences between fresh and old material for small birds and mammals were only 0.2–0.3%.

In conclusion, when studying the diet of the Gyrfalcon, fresh and old prey remains collected at nest sites are of the same value, and they may be combined by nest site and nesting season. Most of the prey items of the Gyrfalcon are identifiable according to bones, not feathers as in the Peregrine, and the bones will be preserved in good condition for years. They decay slowly because of the barren soil and cold climate within the Gyrfalcon's range. Thus, we combined older prey remains with fresh remains in our analyses. We were able to classify the old remains to a specific nesting season by knowing exactly the year-to-year occupation and nesting history of each nest area (Koskimies 2011), and by collecting fresh remains as accurately as possible in June just before fledging and, in most cases, again in September after the dispersal of the juveniles.

RESULTS

Diet Composition of the Gyrfalcon During the Breeding Season.—Our total material contains 5,919 prey individuals, of which as much as 89% were either Willow Ptarmigan or Rock Ptarmigan (Table 1). The proportion of *Lagopus* spp. varied annually between 83% and 94% from 1998 to 2010. The percentages of other main prey species were small in comparison to the two ptarmigan species: 2.2% for the Golden Plover (*Pluvialis apricaria*), 1.2% for the Whimbrel (*Numenius phaeopus*), 0.5% for the Hooded Crow (*Corvus corone*), 0.4% for the female Capercaillie (*Tetrao urogallus*), 0.4% for the Long-tailed Jaeger (*Stercorarius longicaudus*), and 0.3% for the Short-eared Owl (*Asio flammeus*). Four other species were found to represent 0.2% each in the diet (10–17 individuals in the total material): Mountain Hare (*Lepus timidus*), Norwegian Lemming, Spotted Redshank (*Tringa erythropus*), and Goldeneye (*Bucephala clangula*). At least part of the frogs (0.4% of prey individuals) may have been caught by Ravens or Rough-legged Buzzards that occupied the same twig nests in earlier years. In addition, there were still 39 other species found in the prey remains in the Gyrfalcon nest-sites but most of them only occasionally, with 1–8 individuals in total (less than 0.015% of prey remains collected).

According to systematic groups, the percentage of waders (5.0%, 10 species) was the biggest after *Lagopus* spp., that of waterfowl (*Anatidae,* 11 species) 1.2%, and of crows (*Corvidae*) 0.7%, respectively. Eight mammal species, in total, represented only 1.5% of the prey individuals.

The diet composition of the Gyrfalcon was analyzed according to mass of the prey species from 1998 to 2002 by Koskimies and Sulkava (2002). The dominance of the *Lagopus* spp. was only a little larger by mass (89% on aver-

Table 1. The annual diet (% by number) of the Gyrfalcon in northern Fennoscandia according to the prey remains collected at the nest sites in the years 1998–2010.

Year	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Anatidae	0.9	1.3	-	1.6	0.9	0.3	1.0	0.5	1.4	1.2	3.2	1.1	2.1	1.1
Raptors	0.4	1.3	-	-	-	0.3	0.2	0.1	0.2	0.6	1.1	-	2.1	0.4
Lagopus spp. ad.	88.9	84.8	92.0	82.6	85.6	84.5	90.7	94.3	92.5	89.4	82.7	94.4	88.7	89.5
Other tetraonids	-	0.7	-	3.2	0.9	0.6	0.3	0.1	0.4	0.3	0.1	-	-	0.6
Waders	5.8	5.3	8.0	8.6	6.2	5.8	3.0	2.2	4.1	4.5	5.0	-	7.2	4.5
Gulls and skuas	1.8	2.0	-	1.0	0.9	0.9	0.3	0.3	0.6	0.7	-	2.2	-	0.7
Corvidae	0.4	3.3	-	1.9	0.9	0.5	0.6	0.3	0.2	0.3	-	1.1	-	0.6
Turdidae	-	-	-	0.3	1.6	0.4	0.4	-	0.2	0.4	-	-	-	0.4
Small passerines	-	-	-	-	0.5	-	-	-	0.2	0.1	-	-	-	0.1
Mountain hares	-	-	-	0.3	0.5	0.3	0.2	0.1	-	0.5	0.7	-	-	0.3
Voles and lemmings	1.3	-	-	-	0.5	0.4	0.8	0.1	-	1.6	5.0	1.1	-	0.9
Other mammals	0.4	0.7	-	-	0.5	0.3	0.4	0.3	-	0.4	-	-	-	0.3
Frogs	-	0.7	-	-	0.5	0.4	1.0	1.1	-	-	-	-	-	0.4
Fish	-	-	-	-	-	0.1	0.2	0.1	-	-	-	-	-	0.1
Material, n	225	151	25	315	437	793	874	756	508	1370	278	90	97	5919
Samples, n	7	5	1	9	10	17	26	23	24	37	18	4	8	189

age in 1998–2002) than by number of individuals (86%). The percentages of most other bird groups, and also that of mammals, stayed lower by mass than by numbers. For example, the proportion of waders was considerable by numbers in 1998–2002 (6.5%), but (because waders are relatively small) it dropped to 2.8% by mass. Only the percentages of "other tetraonids" (i.e., female Capercaillie) and that of waterfowl were higher by mass than by number, as most species included in these groups are heavier than *Lagopus* spp. In fact, the percentage by mass for *Lagopus* spp. was a little higher than mentioned above (89%), because the masses of *Lagopus* spp. were calculated by Koskimies and Sulkava (2002) according to the average weight of the two *Lagopus* species, although the amount of the Willow Ptarmigan in the falcon diet was actually many times higher than that of the Rock Ptarmigan, and, at the same time, the Willow Ptarmigan is about 7% heavier than the Rock Ptarmigan.

Effect of the Main Habitat Type on the Gyrfalcon Diet.—We classified the Gyrfalcon nest areas into three groups according to the dominant landscape around the nest sites, using a radius of about 10 km. Although breeding Gyrfalcons may hunt 20–30 km from their nest site (Cade et al. 1998, Booms et al. 2008), and although we do not know the actual hunting range, at least a considerable amount of food is probably caught within 10 km from the nest. As the diversity and abundance of various prey species varied according to habitat composition, we considered it reasonable to ask whether or not the type of landscape had any effect on the diet composition of the Gyrfalcon. We admit that our method is rough, but without knowing the real use of various habitats and areas for hunting by falcons, we are not able to examine this question in more detail. We divided our vast study area into three main landscape types, those dominated by (1) open alpine fells, (2) low and mainly sparse birch forests in uplands, on fell slopes and along fairly narrow river valleys, and (3) fairly high and dense pine forests (Table 2).

Table 2. Diet (% by number) of the Gyrfalcons in northern Fennoscandia in the years 1998–2010 classified into five groups according to the three main habitat types (landscape dominated by (1) alpine fell areas, (2) bird forest, (3) pine forest) and three geographical regions (Enontekiö, Utsjoki, Inari). Five sites from Sweden and eight sites from Norway, all near the Finnish border, are included in Enontekiö and Utsjoki, respectively. Only species with over eight individuals among the prey in the total material (n = 5919) are shown (other species grouped together).

Habitat Region	Fell Enontekiö	Fell Utsjoki	Birch Enontekiö	Birch Utsjoki	Pine Inari	Total
Teal, *Anas crecca*	-	-	0.3	0.1	0.4	0.2
Goldeneye, *Buceplala clangula*	-	0.3	0.3	0.1	0.5	0.2
Other waterfowl	0.8	0.3	0.4	0.4	1.3	0.7
Willow Ptarmigan, *Lagopus lagopus*	5.5	9.4	9.2	11.0	7.7	9.2
Rock Ptarmigan, *Lagopus muta*	6.3	4.4	2.9	3.7	0.8	3.1
Lagopus spp.	80.0	76.3	76.2	75.6	76.0	76.2
Lagopus, total	91.7	90.1	88.4	93.1	84.6	89.7
Capercaillie, *Tetrao urogallus female*	0.2	-	-	-	1.4	0.4
Golden Plover, *Pluvialis apricaria*	2.5	1.2	3.7	1.3	2.5	2.1
Whimbrel, *Numenius phaeopus*	1.0	1.5	1.3	0.7	2.2	1.3
Spotted Redshank, *Tringa erythropus*	0.4	-	-	0.0	0.5	0.2
Ruff, *Philomachus pugnax*	0.2	0.6	0.3	0.2	0.3	0.3
Other waders	0.4	0.6	0.6	0.5	1.2	0.7
Long-tailed Skua, *Stercorarius longicaudus*	0.2	2.3	0.1	0.3	0.1	0.3
Larus spp. and *Sterna* spp.	-	-	0.3	0.4	0.6	0.4
Short-eared Owl, *Asio flammeus*	0.2	0.3	0.1	0.1	0.6	0.3
Hooded Crow, *Corvus corone*	0.2	-	0.5	0.3	1.0	0.5
Thrushes, *Turdus* spp.	0.4	0.3	1.0	0.1	0.5	0.4
Small passerines	-	-	0.4	0.4	-	0.2
Other birds	-	0.3	0.3	0.2	0.6	0.3
Mountain hare, *Lepus timidus*	0.4	0.3	0.3	0.3	0.1	0.2
Norwegian lemming,*Lemmus lemmus*	0.6	0.3	0.3	0.4	0.1	0.3
Other voles	-	-	0.8	0.6	0.4	0.5
Ermine, *Mustela erminea*	-	-	0.5	0.2	0.1	0.2
Other mammals	0.6	0.6	0.1	0.2	0.1	0.2
Frogs	0.4	1.2	0.3	0.0	0.8	0.4
Fish	-	-	-	-	0.3	0.1
Material, n	524	342	783	2279	1541	5469
Nest sites, n	4	8	9	17	8	46

The third type was found only in Inari, northeastern Lapland, but the first and second types were also divided regionally into two areas, Enontekiö in northwestern Lapland, and Utsjoki in northern Lapland.

The diet of the Gyrfalcon did not vary much by landscape and by region, as the dominance of the Willow Ptarmigan and the Rock Ptarmigan was so high everywhere. The total percentage of *Lagopus* spp. varied between 84.6% and 91.7%, and that of waders (the second largest group) from 2.7% to 6.7%, from one landscape type and region to another (Table 2). Some of the differences were, however, statistically significant (χ^2 contingency table, StatView®). The northeastern Inari region, dominated by pine forests, differed most from the other four regional landscape types: the percentage of *Lagopus* spp. was smaller (88–92%), but that of waders and waterfowl larger (e.g., compared to the neighboring birch forest in Utsjoki; for the waders $\chi^2 = 31.21$, and for waterfowl $\chi^2 = 8.79$, $p < 0.001$ and 0.003, respectively). Mammals (mainly voles) were eaten more often in the birch forest of Utsjoki than in the pine forest of Inari (χ^2 = 4.54, p = 0.033). There were no significant differences within the alpine fell areas, but in the birch forest area in Enontekiö, Gyrfalcons ate fewer ptarmigan but more waders than in the similar habitats in Utsjoki (χ^2 = 16.53 and 14.95, p < 0.001). In Finland, with a very detailed knowledge of the distribution and density of all the bird species (Väisänen et al. 1998), in the future it will be possible for us to analyze differences in the relative availability of all the suitable prey species by region and landscape type.

Annual Changes in the Diet.—Differences in diet composition among the years were relatively small, similar to the regional variation, as stated in the previous section. The percentage of *Lagopus* spp. varied from 78.7% to 94.0% in 1998–2009 (71.8% in the small material from 2010 excluded), and that of waders 2.3–9.8% (in 2010 15.4%). Some of the annual changes were, however, significant. In the years 1999 and 2006, the percentage of *Lagopus* spp. decreased from the previous year by 11.4% and 4.3%, respectively (χ^2 = 4.17 and 7.73, p = 0.041 and 0.0054, respectively). In the year 2004, the percentage of *Lagopus* spp. increased from the previous year by 5.2% (χ^2 = 9.51, p = 0.002). In the smaller proportion of waders there was only one significant change: in 2004 the percentage decreased by 5.1% from 2003 (χ^2 = 18.28, p < 0.001). The numerically large changes in 2010 were not significant (because of the small sample of material, only 97 prey items collected due to the absence of most pairs), but probably they indicate real fluctuations in diet composition, as the populations of both *Lagopus* species were extremely low (Koskimies 2011). But until the year 2010, the evenness of the percentage of *Lagopus* spp. was notable, in spite of nine-fold fluctuations of the two ptarmigan populations during our study period (Koskimies 2011).

Gyrfalcon Diets in Nest Areas of Different Breeding Activity.—During our study period (13 years) many nest areas were occupied only in one or two years, but several others were occupied more often. In the areas of alpine fells and in the birch forest area in Utsjoki, northern Lapland, for example, Gyrfalcons bred in four nest areas from three to six years (of 13), and in about ten nest areas only once or twice. The diets of the falcons were very similar in these nest areas with both types of occupation frequency: the proportion of *Lagopus* spp. was 93.3% in more regularly occupied territories, and 93.0% in less frequently occupied ones. The percentage of waders was 2.1% vs. 3.4%, and that of mammals, 1.2% and 2.0% respectively. There was, however, a difference in the proportion of Rock Ptarmigan in the diet: it was 30.1% of the total number of *Lagopus* spp. in more regularly occupied territories but only 14.0% in the less popular ones; the difference was statistically significant (χ^2 = 8.78, p = 0.003, total materials 1,195 and 1,015 prey individuals). Also in alpine fell landscapes in Utsjoki and Enontekiö (572 prey individuals in regularly occupied nest areas vs. 259 in less frequently occupied) the diets did not differ: the percentage of *Lagopus* spp. was 92.0% vs. 89.6%, and those of waders, 3.7% vs. 5.8%, and mammals, 1.7% vs. 0.8%, respectively. On alpine fells, the pairs occupying the more popular nest areas hunted a higher proportion of Rock Ptarmigan (54.5% of total *Lagopus* spp.) than those nesting in less frequently occupied nest areas (26.1%; this difference was also significant: χ^2 = 4.66, p = 0.031).

Based on this comparison, we conclude that the availability of Rock Ptarmigan, in addition to good numbers of Willow Ptarmigan, increased the quality and popularity of a nest area both in the alpine landscapes and close-by areas dominated by birch forests. The Rock Ptarmigan is an unevenly distributed and fairly uncommon species in Finland, with the densest population on the highest fell tops in western and northern Utsjoki and northwestern Enontekiö (Väisänen et al. 1998). Only some Gyrfalcons nest close to Rock Ptarmigan habitat, and if they do, this species may be a preferred prey especially during the Willow Ptarmigan population lows, because the amplitude of cyclical fluctuations of the Rock Ptarmigan population is not as large as that of the Willow Ptarmigan (Väisänen et al. 1998).

All eight pairs breeding in Inari, northeastern Lapland (dominated by pine forests) nested more often than the pairs at higher altitudes in Utsjoki and Enontekiö – from three to seven years of the 13 years of this diet study period. Unlike the Gyrfalcons of the alpine fells and birch forest, these falcons, hunting presumably in sparse and low pine forests bordered by birch forest, caught mostly Willow Ptarmigan (of the total *Lagopus* spp., 90.2% were *L. lagopus* Willow Ptarmigan and only 9.8%, *L. muta*, respectively). Thus, availability of the Willow Ptarmigan is an absolute prerequisite for breeding of the Gyrfalcon in these areas where there are no or only small alpine fell tops inhabited by a few Rock Ptarmigan.

In addition to food, availability of a secure nest site was of utmost importance for high-quality Gyrfalcon nesting habitat (Koskimies 1999, 2006a, 2011, Cade et al. 1998, Booms et al. 2008). The higher frequency of nesting in Inari was partly explained by the fact that in many parts of this area there were more and better quality cliff faces for falcons (and Ravens) to nest on than in many parts of Utsjoki and Enontekiö. Thus, availability of ptarmigan species was of great value for Gyrfalcons to survive and reproduce, but there were also other factors which must be taken into account when interpreting the quality of a habitat type or geographical area for the species. The final result to be seen was the enormous variation in the occupation rate of the Gyrfalcon nest areas and nest sites even within a small geographical area and the same habitat type (Koskimies 2011).

The Proportion of Willow Ptarmigan and Rock Ptarmigan in the Diet of the Gyrfalcon.—We identified Willow Ptarmigan and Rock Ptarmigan material according to the lengths of tarsometatarsus and femur bones (see methods). In most samples there were more tarsometatarsi than femurs, but in many samples more femurs were identified as well. In total, 640 (13%) individual *Lagopus* spp. were identified to species level from 1998 to 2008. The identification rate by Nyström et al. (2005) was 14% in northern Sweden. Very few Rock Ptarmigan were identified from 1998 to 2002 (fewer than 20 *Lagopus* spp. by species per year, because of small yearly samples of materials). In the greater yearly samples of materials from the years 2003–2008 (61–153 identified *Lagopus* spp. per year) there were clear annual changes in the percentages of the two species. Some of these yearly changes seem to show that the yearly changes of Rock and Willow Ptarmigan populations may also go in different directions. Statistically significant changes in different directions were the increase of Rock Ptarmigan in 2004 and the decrease in 2006 from the previous year in relation to the Willow Ptarmigan (Rock Ptarmigan 2003–2004, n = 15 and 23, Willow Ptarmigan 2003–2004, n = 59 and 38, $\chi^2 = 4.20$, $p = 0.040$; and Rock Ptarmigan 2005–2006, n = 59 and 17, Willow Ptarmigan 2005–2006, n = 81 and 83, $\chi^2 = 15.90$, $p < 0.001$).

In the period 1998–2008 (n = 640 identified *Lagopus* spp.), the percentage of the Willow Ptarmigan was 73.6% and that of the Rock Ptarmigan was 26.4% of the identified *Lagopus* individuals. With this relation we can calculate the real percentages of these species in the total diet of the Gyrfalcon, as was done by Nyström et al. (2005). According to this calculation the real percentages in the total material of our study were 65.8% Willow Ptarmigan and 23.6% Rock Ptarmigan. Thus, in our study area, Willow Ptarmigan was absolutely the main prey species during the breeding season and for raising the young, and for most falcons probably, in general, the only food item from autumn to spring.

Table 3. Diet of the Gyrfalcon (% by number of prey individuals) in Fennoskandia according to materials of over 400 prey items per study. Lang = Langvatn 1977, Lind = Lindberg 1983, Nyst = Nyström et al. 2005, Haft = Haftorn 1971, Kosk = Koskimies (this study), Huht = Huhtala et al. 1996 (Salla), Kish = Kishchinskiy 1958.

	Lang	Lind	Nyst	Haft	Kosk	Huht	Kish
Anatidae	0.4	1.3	0.3	0.2	1.1	1.2	2.0
Lagopus lagopus	-	4.5	2.3	25.3	8.7	-	-
Lagopus muta	-	4.8	10.0	0.8	2.9	-	-
Lagopus spp.	84.0	57.9	73.5	70.7	77.8	52.1	38.0
Lagopus total	84.0	67.1	85.9	96.8	89.5	52.1	38.0
Other tetraonids	-	0.6	-	-	0.6	5.4	-
Charadriidae and *Scolopacidae*	2.1	0.8	0.7	1.6	4.5	23.6	5.0
Laridae and *Stercoraridae*	-	0.3	-	0.2	0.7	0.2	7.8
Corvidae	2.6	1.5	0.3	0.3	0.6	1.4	0.3
Turdidae	1.1	0.4	0.1	0.1	0.4	3.8	0.6
Small passerines	0.6	0.1	-	0.1	0.3	1.4	1.3
Other birds	4.1	1.1	-	0.6	0.1	3.0	3.1
Birds, total	94.9	73.2	87.3	99.8	97.8	92.2	58.1
Lepus timidus	0.4	0.6	-	-	0.3	1.6	0.7
Lemmus lemmus	0.6	14.8	9.6	-	0.3	0.6	23.2
Other voles	3.2	10.2	3.2	-	0.6	4.2	12.0
Other mammals	0.9	0.6	-	0.2	0.3	0.8	1.3
Mammalia, total	5.1	26.2	12.8	0.2	1.5	7.2	37.3
Other prey	-	0.6	-	0.2	0.5	0.4	4.6
Material, ind.	468	1410	900	1252	5921	499	702

Discussion

In Fennoscandia, seven studies on the diet of the Gyrfalcon have been published so far with more than 400 identified prey individuals in each of them (Table 3). Most of them have been made inland, in open mountain tundra and in mountain birch forest zones. The two *Lagopus* species (Willow Ptarmigan and Rock Ptarmigan) were the main prey of the Gyrfalcon in all of the studied areas, often summing from 85% to 90% of the total number of individuals. The even higher percentage (97%) published by Haftorn (1971) may be an artifact, as his material was one large sample from a nest occupied for a very long time and it lacked pellets, which usually include a higher than average proportion of smaller prey species.

The lower proportion of *Lagopus* spp. reported by Kishchinskiy (1958) and Lindberg (1983) can be explained by a high proportion of Norwegian Lemmings and other voles; the lemming populations were at the highest level during their study periods, and in such years Gyrfalcons frequently hunt these small mammals (e.g., Cade et al. 1998, Booms et al. 2008). Although the Gyrfalcon has been considered as an obligate bird hunter, the proportion of lemmings, Arctic Hares (*Lepus arcticus*) and other small- and medium-sized mammals may comprise up to almost two-thirds of the prey items, especially in the High Arctic (Cade et al. 1998, Nielsen 2003, Booms et al. 2008), showing the relative flexibility of Gyrfalcon hunting habits as circumstances dictate. In addition, Kishchinskiy (1958) reported a high number of larids in the food of the Gyrfalcons breeding close to water on the Kola Peninsula (Table 3). Similarly, Nielsen and Cade (1990) and Nielsen (2003) found in Iceland that the nearer to a lake or sea coast a Gyrfalcon pair bred, the higher was the proportion of waterfowl, larids, auks, and other shorebirds and seabirds. Diet composition varied annually and regionally on a wider geographical scale in Iceland, depending on the relative abundance of the suitable prey species from year to year and from region to region (Nielsen and Cade 1990, Nielsen 1999, 2003).

The ability of Gyrfalcons to adapt their hunting tactics to local conditions has been shown earlier also in Finland by Pulliainen (1975) and Huhtala et al. (1996): in a lone nest area in eastern Lapland, farther south from our Inari study area, but also dominated by pine forest, the percentage of *Lagopus* spp. was only 53% (markedly lower than in our study), and that of waders as high as 24%. Despite these local exceptions, the diet of the inland Gyrfalcon pairs in northern Fennoscandia was very evenly dominated by the two *Lagopus* species, without any marked changes either from one main landscape type to another or from year to year. In Finland, the populations of Willow Ptarmigan and Rock Ptarmigan decreased catastrophically in the years 2007–2010 (Paasivaara et al. 2010, Koskimies and Ollila 2009, Koskimies 2011), but still their proportion in the diet of the Gyrfalcon decreased only by 2.9% (from a mean of 90.9% in 1998–2006 to a mean of 88.0% in 2007–2010). This decrease was, however, statistically significant based on our large sample ($\chi^2 = 10.48$, $p = 0.0012$).

Hagen (1952) thought that the Gyrfalcon was specialized to hunt on *Lagopus*, regardless of other prey species' availability. Later Langvatn and Moksnes (1979) proposed that the Gyrfalcon chooses as additional prey other birds of the same size class, and in Iceland the diet of the Gyrfalcon includes much "alternative" prey (e.g., waterfowl), if the Rock Ptarmigan density has markedly decreased (Bengtson 1971). Nielsen (1999, 2003) has studied in detail the effect of Rock Ptarmigan population cycles on the population size and breeding success of the Gyrfalcon, as well as the numerical and functional response of the falcons to their prey. In spite of the potential flexibility of the falcons, Rock Ptarmigan cycles determine significantly the population performance of Gyrfalcons. A similar response by Gyrfalcons to Willow Ptarmigan population cycles seems to exist in northern Fennoscandia (Koskimies 2011), as well as other parts of the Gyrfalcon range in the Old (Cade et al. 1998) and New World (Booms et al. 2008).

The ultimate reason for the absolute dependence of the Gyrfalcon on ptarmigan for survival and reproduction was the virtual lack of other suitable prey from late autumn to late spring in the inland arctic and subarctic parts of their wintering range. The Gyrfalcon lays eggs in late March or early April, weeks before the major flocks of migratory birds start to arrive in Lapland. Although in May and June there was a growing number of other appropriate prey available, our study and the previous ones show that parent falcons hunted *Lagopus* spp. to feed their young; Table 3 shows diet composition during the breeding cycle included ptarmigan at least up to June or early July when the young falcons fledged. In our study, prey items have also been collected in the majority of nest areas in early autumn, and thus, our statistics also include the prey eaten by fledged juveniles in July, while they returned to feed at the natal nest or close to it for some weeks (e.g., Cade et al. 1998). Actually, the fledging time of the falcons coincided with the weeks when there is the maximum number of flightless or poorly flying young of both ptarmigan and other birds, like waders, waterfowl, gulls and thrushes, among others. The juvenile falcons have the highest potential for learning to hunt in July and August before the young prey birds become independent and start their autumn migration, as Cade (1960) pointed out for Gyrfalcons in Alaska. A long practice period and good hunting skills are necessary for the juvenile falcons to survive their first winter when only ptarmigan are available as prey until the next summer, if they are going to stay inland in northern Fennoscandia, as some of them seem to do for at least part of the early or late winter. Most of the young, however, probably move westward to get closer to coastal areas with plenty of other prey like waterfowl, gulls and waders (Koskimies 2011). Almost all adult territorial falcons, however, try to stay close to their nest sites throughout winter, but are forced to wander more widely during the population lows of the two ptarmigan species (Koskimies 2011).

One may conclude that the Gyrfalcon has evolved a strong "search image" for *Lagopus* spp. (Cade 1960) from the exceptionally high percentage of only one or two prey species almost throughout the year, and the dominance of this food type up to late June for feeding young, in spite of a fairly high density especially of waders throughout the Gyrfalcon's range. This might be reinforced during the cold and partly dark period from autumn to spring by repeated, successful hunting as the falcons, with no alternative prey, have to become more and more effective. The migratory birds appear, behave, and sound quite different from ptarmigan, and to an exceptionally specialized hunter like the Gyrfalcon, they serve as food only in the case of an extraordinary population low of *Lagopus* spp.

In different areas, however, the diet of the Gyrfalcon may vary, depending mainly on the abundance of alternative prey. For example, the percentage of *Lagopus* spp. eaten by a Gyrfalcon pair studied by Dementiev and Gortchakovskaya (1945) on an island near the coast of the Kola Peninsula was astonishingly low, only 3.4%; the main food sources at this nest were seabirds and Norwegian Lemmings. Also, in arctic North America, mammals (Ground Squirrels *Spermophilus undulatus* or Arctic Hares), and in Greenland, Snow Buntings (*Plectrophenax nivalis*) and other small passerines as well as hares and Collared Lemmings (*Dicrostonyx groenlandicus*) have been recorded among the most numerous prey species (Cade 1960, Burnham and Mattox 1984, Poole and Boag 1988, Booms and Fuller 2003, Booms et al. 2008).

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