

Golden Eagles on the Swedish mountain tundra – diet and breeding success in relation to prey fluctuations

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We studied the diet and the relationship between prey density fluctuations and breeding success of a Golden Eagle (*Aquila chrysaetos*) population on the mountain tundra region of northern Sweden. We used a new PCR based method to analyse the DNA in bone fragments from Golden Eagle prey remains. This allowed us to accurately identify the Ptarmigan species that the bone fragments originated from, and hence, establish the proportions of Ptarmigan species in the eagle's diet. We could conclude that Ptarmigan species (*Lagopus* spp.) are the most important prey category for this Golden Eagle population (63% of all identified prey), and that Willow Ptarmigan (*L. lagopus*) occurred more frequently in the diet than Rock Ptarmigan (*L. mutus*) did (Willow Ptarmigan 38%, Rock Ptarmigan 25%). Other important prey included reindeer (*Rangifer tarandus*), mountain hare (*Lepus timidus*) and microtine rodents. The Golden Eagles managed to maintain a relatively broad food niche, despite an environment with low prey diversity. Microtine rodents, hare and Ptarmigan populations showed similar population fluctuations in the study area. The breeding success of the Golden Eagles showed a strong relationship to the yearly density index of the most important prey category, the Ptarmigan species.



1. Introduction

Small herbivores (e.g. microtine rodents, Tetraonid birds and hares) of arctic and northern boreal communities are known for their cyclic population

fluctuations (Hörnfeldt 1978; Angelstam *et al.* 1985; Hörnfeldt *et al.* 1986; Lindström *et al.* 1987), and the predators in these communities are expected to respond both functionally and numerically to these prey population cycles (Elton 1924;

Lack 1954; Hanski *et al.* 1991; Boutin 1995; Hanski & Korpimäki 1995; Oksanen *et al.* 2001).

The Golden Eagle (*Aquila chrysaetos*) of the boreal region of Fennoscandia can be regarded as an apex predator with a broad food niche. The dominating prey category usually comprises the Tetraonid (*Tetraonidae*) species, such as Capercaillie, (*Tetrao urogallus*), Black Grouse (*T. tetrix*) and Ptarmigan species (Tjernberg 1981; Högström & Wiss 1992; Sulkava *et al.* 1999). Other important prey are Mountain Hare (*Lepus timidus*) and Reindeer (*Rangifer tarandus*). In addition to these main prey categories, at least 30 bird species appear in smaller amounts in the diet. Golden Eagles also prey on several other predatory species such as mustelids, owls, raptors and foxes (Tjernberg 1981; Högström & Wiss 1992; Sulkava *et al.* 1999).

There are some studies showing how the fluctuations in prey availability affect the diet and breeding success of boreal Golden Eagles. Sulkava *et al.* (1999) showed that Finnish Golden Eagles changed their diets in accordance to both Tetraonid and hare availability. Tjernberg (1983) found that the breeding success of Swedish boreal Golden Eagles followed the population fluctuations of tetraonid birds and hares. However, for Golden Eagles breeding in the northernmost part of Scandinavia, i.e. on the mountain tundra, no studies concerning predator–prey relationships have to our knowledge been published.

This paper concerns a small population of Golden Eagles on the Swedish mountain tundra (67° N, 17° E). The population breeds under harsh conditions, and some important prey species, such as the large Tetraonid species, are absent here (Cramp & Simmons 1980). We investigated the general diet of the Golden Eagle population in relation to the main prey species in the area. We also refined diet studies from prey remains by applying a newly developed DNA identification protocol (Dalén *et al.* 2004; Nyström *et al.* 2006). The method identified the species of Ptarmigan from morphologically indistinguishable bone fragments, allowing us to establish the proportions of different Ptarmigan species in the diet. Further, we investigated the population dynamics of the main prey groups in the study area, and their effects on the breeding success of the Golden Eagle population.

2. Methods

2.1. Study area and the Golden Eagle population

The study area is approximately 4,800 km² and ranges through three national parks of northern Sweden: Padjelanta, Sarek and Stora Sjöfallet in Norrbotten County. The western part of the area comprises a highland plateau surrounding two great lakes: Virihaure and Vastenjaure. Sarek, in the centre of the study area, has more of an alpine character dominated by mountain massifs with glaciers and several peaks over 1,800 m a.s.l. Stora Sjöfallet constitutes the eastern boundary of the study area. It has a varied topography with alpine ranges and low ridges, flat high plains and deeply carved valleys. Dry heath is the dominating vegetation type with an increasing element of Willow bushes (*Salix* spp.) in the more moist areas. The study area lacks infrastructure other than hiking trails, small tourist cabins and some Sámi settlements with few inhabitants. The yearly mean temperature is 0°C and the area is snow-covered 225 days per year.

We surveyed the Golden Eagle population in the study area from 1998 to 2003. The survey was a part of an ongoing monitoring program for Gyrfalcons (*Falco rusticolus*) and Golden Eagles conducted on behalf of the County board of Norrbotten. We performed two surveys each year. The first survey lasted from March to May. During this period we used snowmobiles to visit the nest sites in all territories with a known breeding history (N = 23). We recorded whether territories were empty or occupied by a single or a pair of Golden Eagles. During the second survey (June to July), the territories that contained pairs during the first survey were revisited (by helicopter) in order to count the number of breeding pairs in the population (defined as pairs with at least one chick at this stage).

2.2. Diet

The prey remains were collected during the second period of the monitoring program, with complementary collections performed throughout the summer period. Prey remains (both pellets and skeletal parts) were collected from the nests,

perches and plucking sites on the nesting cliff. We identified the species with help of a reference collection of bones, teeth, fur and feathers. We mostly used teeth morphology to identify the species of microtine rodents. Feathers could be identified to species in most cases, and skeletal remains from birds were identified to order or genus level. We calculated the minimum number of specimens for each prey category. These figures were divided with the total prey number in order to yield the proportions of different prey categories in the diet.

There are two Ptarmigan species in the study area, Rock Ptarmigan and Willow Ptarmigan. When occurring as prey remains, these two species are often indistinguishable due to similar morphologies (unspecified Ptarmigan species are hereafter referred to as "Ptarmigan"). The best cues come from the metatarsus that significantly differs in length between the Ptarmigan species (Myrberget 1977). However, our prey collections contained few intact metatarsi and, therefore, we used a new DNA identification protocol designed by Dalén *et al.* (2004) which has been used successfully to identify the different Ptarmigan species in the diet of the Gyrfalcon in the study area (Nyström *et al.* 2006). The PCR protocol utilises two species-specific primers (one Rock Ptarmigan primer and one Willow Ptarmigan primer) in combination with one general primer. The species-specific primers are designed to anneal at different distances from the general primer and thus result in PCR products of different size depending on which species the DNA extract originated from. The PCR products are scored on an agarose gel and assigned to either Rock or Willow Ptarmigan depending on the size of the PCR products. We applied the method on bone fragments originating mostly from pellet contents. However, we analysed only one bone fragment from each pellet. We used a drilling machine to obtain 30 mg of bone powder from each bone fragment. A total of 126 samples were used for DNA extraction, using the DNeasy tissue kit (Qiagen). Five μl of the DNA extracts were used in 25 μl single tube PCRs following Nyström *et al.* (2006).

2.3. Prey density

We estimated the relative availability of Ptarmigan, hares and microtine rodents in the study area during the period 1998 to 2003 (microtine rodents 1998–2003, Ptarmigan and hare 1999–2003). All density estimates were performed during the period 1 July to 15 August. The relative densities of Ptarmigan and hare were estimated from dropping counts. The dropping counts were performed during walked transects with a fixed strip width of one meter in each direction. The short width of the strip ensured that all droppings inside the strip could be detected, regardless of the substrate. Ptarmigan and hare droppings fragment relatively easy, and there is therefore little risk of encountering old droppings (i.e. from earlier years). Older droppings are usually destroyed during the winter and especially during the melting period. Droppings can, however, remain intact in rock cavities, such droppings were therefore not included in our protocols. We also recorded all Ptarmigan and hares seen during the transect sampling events. The droppings had to be spaced at least half a meter from each other to be regarded as single objects, thus two droppings within a distance shorter than half a meter were recorded as one object. From this follows that piles of droppings were also treated as single objects. The strip transects were placed in open habitats and in the altitude interval of approximately 400–1,300 m a.s.l. This altitude interval ranges from the bottom of river valleys up to the altitude where the vegetation ceases. The transects were concentrated in Golden Eagle breeding territories; typically the greater river valleys with their surrounding mountain sides. These areas were also inhabited by several other predators, such as Gyrfalcon, Rough-Legged Buzzard (*Buteo lagopus*), Arctic Fox (*Alopex lagopus*), Red Fox (*Vulpes vulpes*) and Wolverine (*Gulo gulo*). In total, 613 km of transects were walked with an effort of 70–160 km each year. The results from the density estimates were presented as number of droppings per km. The actual sizes of the Ptarmigan and hare populations in the study area were unknown.

The abundances of microtine rodents were estimated with snap trapping events. We used standard mice snap traps baited with raisins and our methods followed Myllymäki *et al.* (1971a; 1971b), with some modifications. The traps were

placed in squares with sides of 15 m. At each corner, three snap traps were placed within a distance of two meters from the corner. One trap line contained five such squares which were aligned 35 m apart. Typically, one trapping event contained two or three such trap lines and lasted for 48 h (240–360 trap nights). Between 2 and 10 such trapping events were performed each year with a total of 9,800 trap nights. The trap lines were placed in the same areas as the strip transects. All capture results for each year were pooled and the yearly availability of microtine rodents was calculated from the mean number of voles caught per 100 trap nights. The actual density of small rodent populations in the study area was unknown. The results from dropping counts and trapping events were used to calculate relative measures of prey availability (Ptarmigan, hare and microtine rodents) for each year. We will refer to these density estimates as “density indexes” hereafter.

2.4. Statistical analysis

We investigated the relationship between the yearly density indexes of the three prey categories and the number of occupied Golden Eagle territories. We also investigated the relationship between these prey categories and the percentage of Eagle territories containing breeding pairs (i.e. the number of territories containing breeding pairs divided with the total number of monitored territories). Further, we investigated the synchrony between Ptarmigan, hare and microtine rodent population fluctuations in the study area. We used simple regression analyses performed in Statistica 6.0.

3. Results

3.1. Diet

We identified 324 prey items from the total collection of prey remains. The dominating prey category was Ptarmigan, which made up 63.3% of the diet (Table 1). The DNA analyses of unidentified Ptarmigan bone fragments were successful in 86 cases out of 126. Of the 86 samples, 52 were identified as Willow Ptarmigan and 34 as Rock Ptarmigan. Thus, of the 63.3% Ptarmigan species, 38.3%

Table 1. The general diet of the Golden Eagle breeding population is presented. The ratio between Rock and Willow Ptarmigan was calculated from the DNA analysis of 86 bone samples. The number of bone samples belonging to each species is shown within brackets. Prey categories are presented as percentage of the total number of prey items (N = 324).

Prey species	No. of prey	%
<i>Birds</i>		
Ptarmigan total <i>Lagopus</i> spp.	205	63.3
Willow Ptarmigan <i>L. lagopus</i>	(52)	38.3
Rock Ptarmigan <i>L. mutus</i>	(34)	25.0
Unidentified Duck	3	0.9
European Kestrel <i>Falco tinnunculus</i>	1	0.3
Short-Eared owl <i>Asio flammeus</i>	2	0.6
Unidentified Thrush <i>Turdus</i> spp.	1	0.3
Raven <i>Corvus corax</i>	10	3.1
<i>Microtine rodents</i>		
Norwegian lemming <i>Lemmus lemmus</i>	35	10.8
Grey-sided vole		
<i>Clethrionomus rufocanus</i>	2	0.6
Field vole <i>Microtus agrestis</i>	1	0.3
<i>Other mammals</i>		
Reindeer <i>Rangifer tarandus</i>	37	11.4
Mountain hare <i>Lepus timidus</i>	19	5.9
Mustelids <i>Mustela</i> spp.	6	1.9
Red fox <i>Vulpes vulpes</i>	1	0.3
Shrew <i>Sorex</i> sp.	1	0.3

constituted Willow Ptarmigan and 25.0% Rock Ptarmigan (Table 1). This made Willow Ptarmigan the most important prey species, followed by Rock Ptarmigan. The third largest prey category was reindeer which made up 11.4%. Norwegian lemmings (*Lemmus lemmus*) constituted 10.8% and mountain hare an additional 5.9% (Table 1). Together these five prey species made up 91.4% of the diet. Of the remaining part, species that could be considered predators made up 6.2% (Table 1). It should be noted that during 2001 there seemed to be quite an increase in the number of microtine rodents in the diet. Of a total of 38 microtine rodents, 20 were found that year. The majority were lemmings.

3.2. The Golden Eagle population in relation to prey population fluctuations

There were on average six times more Ptarmigan droppings than hare droppings per km and year

Table 2. The number of empty and occupied Golden Eagle territories and the number of territories with breeding pairs each year. These figures are also presented as percentage of the number of territories monitored each year. The table presents the number of chicks produced each year, and yearly prey density indexes along with the efforts of prey estimations.

Population parameters	1998	1999	2000	2001	2002	2003
No. empty territories	7	8	2	6	5	7
No. occupied territories	16	12	14	16	18	16
No. of territories with breeding pairs	5	1	3	5	4	5
No. chicks	8	1	5	7	7	5
% empty territories	30.4	40.0	12.5	27.3	21.7	30.4
% occupied territories	69.6	60.0	87.5	72.7	78.3	69.6
% territories with breeding pairs	21.7	5.0	18.8	22.7	17.4	21.7
No. chicks per breeding pair	1.6	1.0	1.7	1.4	1.8	1.0
<i>Prey density indexes</i>						
Ptarmigan/km		1.8	3.6	7.1	4.3	5.6
Hare/km		0.4	0.9	1.2	0.5	0.6
Transect effort (km)		123	121	138	161	70
Microtine rodents (per 100 trap nights)	0.8	0.0	3.3	5.0	0.3	0.7
Trapping effort (100 trap nights)	25.2	4.8	25.2	25.2	10.4	7.2

(Table 2). However, the two prey populations fluctuated within similar amplitude intervals where Ptarmigan varied 4-fold and hares 3-fold between years (Fig. 1). We only observed one hare in the study area during the entire period. We frequently encountered Ptarmigan during the transect events, but rarely managed to identify their species. Of 39 successful identifications, 19 were Willow Ptarmigan and 20 Rock Ptarmigan. The number of observations of Ptarmigan (and hare) each year was highly weather dependent.

Microtine rodents were caught with an average of 1.7 individuals per 100 trap nights and the population showed a 5-fold density index variation between years (Fig. 1). The most abundant rodent species was the Grey-sided Vole (*Clethrionomus rufocanus*). Lemmings appeared in the study area on two occasions, they were present in small numbers in 1998 and in large numbers in 2001. Ptarmigan, hare and microtine rodents showed similar population trends over the period. Low densities during 1999 were followed by a steady increase towards 2001 when all populations peaked. After a decrease in 2002, all populations began to increase again in 2003 (Fig. 1). There were no significant relationships between Ptarmigan fluctuations and any of the other two prey population fluctuations ($r^2_{\text{hare}} = 0.54$, $r^2_{\text{vole}} = 0.39$). However, there was a significant relationship between hare and vole po-

pulation dynamics ($r^2 = 0.98$, $n = 5$, $P < 0.002$, Fig. 1). Log transformation of the prey density indexes did not produce any further significant relationships between the population trends.

We monitored the Golden Eagle population from 1998 to 2003, although the number of territo-

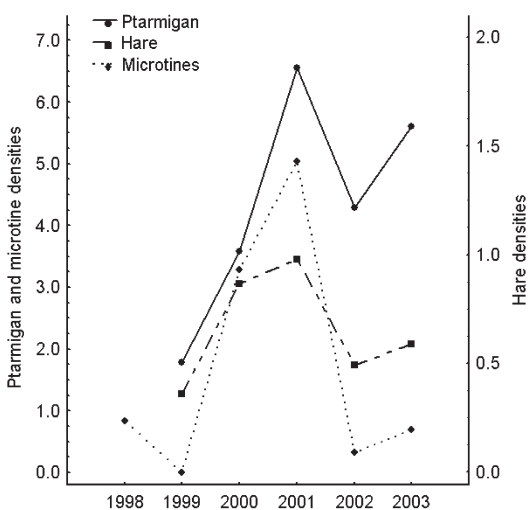


Fig. 1. The prey fluctuations in the study area, i.e. Ptarmigan hare, and microtine rodent population trends over the study period. Population trends are based on the prey density indexes (hare and Ptarmigan droppings/km, microtines/100 trap nights).

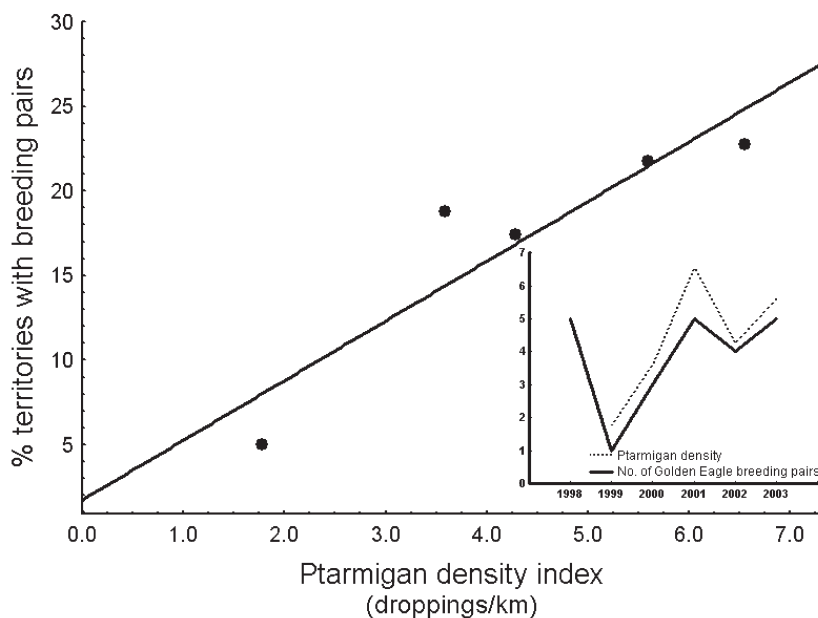


Fig. 2. Percentage of territories containing Golden Eagle breeding pairs each year, in relation to the ptarmigan density index in the study area. The inserted figure shows the number of breeding pairs in relation to ptarmigan density as a time series.

ries monitored each year varied to some extent (Table 2). Of the 23 known breeding territories, 22 were occupied at least once during the entire period. The number of occupied territories each year varied between 12–18, or 60–87.5% of the number of territories monitored (Table 2). The Golden Eagles bred 23 times during the period. These breeding events occurred in 13 different territories, and the 23 Golden Eagle pairs produced 33 chicks. The number of breeding pairs each year varied from one to five or 5.0–22.7% of the number of monitored territories (Table 2).

No relationship was detected between the number of occupied territories per year and any of the yearly prey density indexes. However, there was a significant relationship between the percentage of territories containing breeding pairs and the yearly Ptarmigan density indexes, showing that the breeding success of the Golden Eagle population was affected by the availability of its main prey ($r^2 = 0.79$, $n = 5$, $P < 0.05$, Fig. 2).

4. Discussion

This study shows that the general preference for Tetraonid birds as prey, which is typical for Nordic boreal Golden Eagle populations (Tjernberg 1981; For Norway, see Högström & Wiss 1992; Sulkava

et al. 1999), also exists in a tundra breeding population of northernmost Sweden. This is somewhat striking, as two important prey species of the Tetraonid family are absent this far north, the Capercaillie and Black Grouse (Cramp & Simmons 1980). The preference for Tetraonid birds was maintained by a pronounced utilisation of Rock and Willow Ptarmigan, constituting the only two members of the family present in the study area. Tjernberg (1981) made an extensive diet study of the Golden Eagle throughout its entire range in Sweden. The number of prey remains from the northernmost part of the range was, however, limited (123 prey remains), but indicated a Ptarmigan dominated diet as found in our study area. However, he did not distinguish between Willow and Rock Ptarmigan proportions in the Eagle's diet, and to our knowledge, this has not been done before. Our study shows that PCR-based DNA methods are useful tools when identifying species from fragmented prey remains. It is also a useful method when prey species are closely related, making morphological characteristics unreliable. The method has been applied to Ptarmigan prey remains originating from the diets of breeding Gyrfalcons in the study area (Nyström *et al.* 2006). For Gyrfalcon prey remains, the method of DNA identification was successful in 90% of the cases. However, when we applied the same

method on the Ptarmigan bones from the Golden Eagle diets, the success rate was only 68%. This was likely due to the fact that Ptarmigan bones from the Golden Eagle's prey remains constituted small bone fragments found in the pellets, whereas the DNA analyses on gyrfalcon Ptarmigan remains were largely based on whole bones, and thus containing more intact DNA.

It was surprising that Willow Ptarmigan constituted a greater part of the diet than Rock Ptarmigan did. Willow Ptarmigan is expected to be relatively rare in our study area (Nyström *et al.* 2006), as it generally prefers lower altitudes with denser vegetation (Cramp & Simmons 1980). This could indicate that the Golden Eagle has a true preference for this species, i.e. that it exploits Willow Ptarmigan to a larger extent than expected from its relative abundance (see e.g. Taylor 1984 p. 97). Although the total diet material was too small to allow any extensive analyses of how local prey availability affected individual Eagles, it was clear that the Eagles in the southernmost part of the study area had a greater proportion of willow ptarmigan in their diets than Eagles in the northernmost part of the study area. This probably reflected a greater availability of Willow Ptarmigan in the southern areas, as it is closer to the coniferous region and therefore more a Willow Ptarmigan habitat.

The Golden Eagles in the study area preyed on reindeer to the same extent as eagles in other regions within the reindeer husbandry area. However, the proportion of hare was unusually small (Tjernberg 1983; Sulkava *et al.* 1999). Still, the total proportion of mammals in the diet was comparable to that of boreal eagles, as the Golden Eagles in the study area also utilised microtines (11%). Keeping in mind the small sample size, it is still worth noting that more than half of all remains from microtine rodents were found during 2001, and the majority of these were lemmings. This was a peak year in the microtine cycle when lemmings reached high densities, so it might be that the Golden Eagle responded functionally to this increase in lemming densities, despite the fact that Grey-sided Voles reached even higher densities in the study area. This could indicate a preference for lemmings, and/or depend on the fact that lemmings are easier to catch due their conspicuous coloration (Andersson 1976) and lesser mobility

than e.g. Grey-sided Vole (Oksanen 1993).

The number of occupied Golden Eagle territories in the study area was unaffected by prey population fluctuations. This was not surprising as Golden Eagles in the study area are resident and highly territorial, limiting population growth even during good food conditions (Brown & Watson 1964; Newton 1979; Steenhof *et al.* 1997). The proportion of breeding pairs in the population, however, significantly tracked the population fluctuations of the main prey. This relationship has also been shown for Alaskan Golden Eagles (McIntyre 2002), and Tjernberg (1983) concluded that the number of breeding pairs in northern Sweden depended on the total amount of hare and four species of tetraonid birds. The same pattern occurred in our study area, with the difference that the breeding success depended on a smaller set of prey species, Rock and Willow Ptarmigan.

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Maakotka Ruotsin tundralla – saaliseläinten kannanvaihtelujen vaikutus ruokavaliioon ja pesintämenestykseen

Tutkimme maakotkan ruokavaliota ja saaliseläinten kannanvaihtelun vaikutusta pesintämenestykseen Pohjois – Ruotsin vuoristoisella tundralla. Käytimme uutta PCR-menetelmää saaliseläinten luiden analysoimiseksi. Näin saimme selville riekkojen ja kiirunoiden osuudet kokonaissaaliista. Riekot ja kiirunat muodostivat suurimman osan maakotkapopulaation saaliista (63 % tunnistetuista saaliseläimistä). Riekon ja kiirunan osuudet kokonaissaalimäärästä olivat 38 % ja 25 %. Muita

tärkeitä saaliseläimiä olivat poro, metsäjänis ja myyrät. Myyrät, jänikset, kanalinnut noudattelivat samankaltaisia kannanvaihteluita tutkimusalueella. Kotkan pesintämenestys korreloi voimakkaasti vuosittaisen kanalintuindeksin kanssa.

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