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Prey selection and prey handling in two raptors  
during the breeding season as revealed by the  
use of video monitoring

Byttedyrvalg og byttedyrhåndtering hos to  
rovfugler i hekkeperioden, avslørt ved bruk av  
videoovervåking

Ida Dihle



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## ABSTRACT

I video monitored one nest of each of two avian predators, namely the rough-legged buzzard (*Buteo lagopus*) and the golden eagle (*Aquila chrysaetos*), in Oppland county, southern Norway, during May-August 2014, to analyse the composition of the diet and the handling of prey items. Of the 120 prey items recorded delivered at the golden eagle nest, mountain hare (*Lepus timidus*) was the most important prey species in terms of mass, with 65 % of the gross body mass of the prey delivered. Grouse (Tetraonidae sp.) was also important, the three species recorded together made up 22 % of the gross body mass in the golden eagle diet. This was in accordance with previous studies. However, a surprisingly large proportion of the diet of the golden eagle consisted of microtine rodents (voles and lemmings). In fact, 51 % of the delivered prey items were microtine rodents. In the region of my study area 2014 was a year with extremely high densities of microtine rodent, and my results may indicate that the golden eagle responds functionally to microtine rodents. The absence of ungulates among the items delivered at the golden eagle nest fits with the results from another golden eagle nest video monitored in Norway, but contrasts from most previous studies made on the diet of the golden eagle by traditional analyses of prey remains in the nest. Of the 253 prey items recorded delivered at the rough-legged buzzard nest, the most important prey in terms of both body mass and numbers was *Microtus* voles, which made up 71 % of the items delivered at the nest. Various other small prey were also utilized, in particular thrushes (*Turdus* sp.), but to a much smaller degree. The diet of the rough-legged buzzard suggests that this raptor responds functionally to *Microtus* voles, which is consistent with results from previous studies. In both raptors studied the male delivered most prey at the nest, while the female brooded and fed the nestlings. The female stayed at the nest feeding the nestlings a longer part of the nestling period than expected. This may be due to the fact that prey were abundant and that the prolonged stay was a strategy to enhance the female's own fitness and thereby future survival. The probability that the nestlings would feed unassisted increased with their age, and with decreasing size of the prey item that was delivered at the nest. The rough-legged buzzard nestlings was also more likely to feed unassisted at low ambient temperature, and when the prey delivered was a mammal rather than a bird. The extent to which the various prey are included in the diet of the golden eagle and the rough-legged buzzard seems to be a result of their varying availability in time and space.

## S A M M E N D R A G

I løpet av mai-august 2014 har jeg i dette studiet videoovervåket et reir av fjellvåk (*Buteo lagopus*) og et reir av kongeørn (*Aquila chrysaetos*), i Oppland fylke, Sør-Norge, for å analysere sammensetningen av diett og håndtering av byttedyr hos de to rovfuglene. Av de 120 byttedyrene registrert levert på kongeørnreiret, var hare (*Lepus timidus*) det viktigste byttedyret i forhold til biomasse, med 65 % av brutto biomasse av alle de leverte byttedyrene. Hønsefugl (Tetraonidae sp.) var også viktig, de tre artene registrert utgjorde tilsammen 22% av brutto biomasse i kongeørnas diett. Dette var i overensstemmelse med tidligere studier. En overraskende stor andel av dietten til kongeørna bestod av smågnagere. Så mye som 51% av de leverte byttedyrene var en smånager i stumpmusfamilien. I regionen som omfatter mitt studieområde var 2014 et år med ekstremt høye tettheter av smågnagere, og mine resultater kan tyde på at kongeørna responderer funksjonelt på smågnagere. Fraværet av klovdyr blant de leverte byttedyrene på kongeørnreiret er i samsvar med resultatene fra andre kongeørnreir som er blitt videoovervåket i Norge, men er i kontrast til de fleste tidligere studier gjort på kongeørnas diett der man har analysert byttedyrrester i reiret. Av de 253 byttedyrene registrert levert på fjellvåkreiret, var det viktigste byttedyret i form av både biomasse og antall *Microtus* gnagere, som utgjorde 71 % av byttene levert på reiret. Diverse andre små byttedyr ble også levert på reiret, spesielt troster (*Turdus* sp.), men i mye mindre grad. Fjellvåkens diett tyder på at den responderer funksjonelt på *Microtus* gnagere, som er forventet fra tidligere studier gjort på fjellvåkens diett. Hos begge rovfuglartene leverte hannen flest byttedyr til reiret, mens hunnen varmet og føret ungene. Begge hunnene ble i reiret og føret ungene lengre enn forventet. Dette kan tyde på at det var rikelig med byttedyr i området, og at det var en strategi for å styrke hunnens kondisjon og videre overlevelse. Sannsynligheten for at ungene spiste selvstendig økte med ungenes alder, og med avtagende størrelse på byttedyret som ble levert på reiret. Hos fjellvåk påvirket også temperaturen ved levering og om byttet som ble levert var et pattedyr sannsynligheten for at ungene spiste selvstendig. I hvilken grad de ulike byttedyrene inngår i kongeørnas og fjellvåkens diett synes å være et resultat av deres varierende tilgjengelighet i tid og rom.

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## INTRODUCTION

Species interactions among trophic levels play a significant role in an ecosystem (Newton 1998; Berlow et al. 2004; Ives et al. 2005). Within the habitats they occupy, populations are influenced by several environmental and demographic factors that can limit their survival and distribution. For a predator, one of the most important limiting factors is the availability and abundance of prey (Newton 1998). The functional and numeric response of predators thus show strong relationship with densities of their prey (Lack 1954; Preston 1990; Steenhof et al. 1997; Nyström et al. 2006). Such interactions are common in avian predators and their prey. Raptors that specialise in feeding on a narrow set of prey respond stronger to their density changes, than generalists raptors, which have a wider range of alternative prey to utilize when the preferred prey is scarce (Andersson & Erlinge 1977; Hanski et al. 1991)

Two raptors that differ in their specialization is the rough-legged buzzard (*Buteo lagopus*) which is a specialist and the golden eagle (*Aquila chrysaetos*), which is a generalist. The breeding success of the rough-legged buzzard is widely regarded as being highly dependent on the population cycles of small mammals. The rough-legged buzzard specializes in preying on small mammals, with a typical preference for voles and lemmings (*Microtinae* sp.). However, they are known to utilize alternative prey when the preferred prey is scarce. (Sylvén 1978; Hagen 1989; Potapov 1997; Pokrovsky et al. 2012; Hellström et al. 2014; Pokrovsky et al. 2014).

The golden eagle is an opportunistic hunter with a broader food niche than the rough-legged buzzard. There is a close relationship between its breeding success and the cyclic abundance of a handful preferred prey species (Steenhof et al. 1997; Sulkava et al. 1999; Watson 2010). The diet of the golden eagle consists of medium-sized birds and mammals, typically species of grouse (*Tetraonidae* sp.), and mountain hare (*Lepus timidus*). However, thrushes (*Turdus* sp.), lemmings and voles in addition to a variety of other species are also utilized but in smaller numbers (Tjernberg 1981; Collopy 1983; Nyström et al. 2006; Johnsen et al. 2007; Sánchez-Zapata et al. 2010; Watson 2010).

Remains from ungulates such as domestic sheep (*Ovis aries*) and wild reindeer (*Rangifer tarandus*) have been found in the nests of golden eagles. Nyström et al. (2006) estimated that approximately 11 % of the diet of golden eagles in mountain tundra region of northern Sweden was made up by

reindeer. These prey are often new-borns or weak individuals (Tjernberg 1981; Watson 2010). Large amounts are paid to farmers every year as compensation for loss of livestock due to golden eagle attacks, but the real effect of golden eagles on livestock is debated (Warren et al. 2001; Sánchez-Zapata et al. 2010; Bevanger 2013). Across areas in Norway there is seemingly no relationship between population size of golden eagles and amount of compensation paid, which may indicate some weaknesses in the system on estimating causes of loss (Gjershaug & Nygård 2003). To assess the economic damage that the golden eagle can inflict on domesticated livestock research focused on its diet is important. Precise knowledge of the foraging habits of these raptors is key to understand their niche in an ecosystem, and forms a basis to develop well-functioning wildlife management strategies for the species (Gjershaug & Nygård 2003).

Traditionally the knowledge of the diet of raptors has been based on analyses of regurgitated pellets and prey remains in and around the nest. However, studies suggest these methods have several limitations and errors. One important error is the misinterpretation of the proportions of particular prey in the diet (Simmons et al. 1991; Nygård & Grønnesby 2000; Rogers et al. 2005; Slagsvold et al. 2010). Video monitoring at the nest would give a more complete and accurate description of the breeding-season diet (Lewis et al. 2004; Selås et al. 2007; Tornberg & Reif 2007).

Video recordings made at the nest also provide valuable information on the biology and the behavioral traits of the studied species, which previously have been difficult, and highly time consuming to record (Reif & Tornberg 2006). The parental roles of raptors differ from other provisioning birds. In the early stages of the rearing period the male is usually the sole provider of food and female brood and feed the young (Newton 2010; Eldegard & Sonerud 2010). As the nestlings grow, they become able to self-feed, the handling time of small mammalian prey is more rapid than large avian prey that require preparation. So at what time the nestlings are able to feed unassisted may not only depend on their age, but also the size and type of prey that is brought to the nest (Sonerud et al. 2014a).

A growing number of studies have used video monitoring to study raptors. To my knowledge only Reif and Tornberg (2006) has video monitored rough-legged buzzards at the nest. Their aim was to compare results from video recordings with those from prey remains and pellets in Finland. They recorded only 95 hours of video, and identified only 11 prey items. In Japan Takeuchi et al.



(2006) video monitored one nest of the golden eagle by using a telephoto lens on a camera situated 170 m away from the nest.

Skouen (2012) was the first to install a camera at a nest of the golden eagle. Her results from a nest in Telemark county, southern Norway, showed that of the 181 prey delivered at the nest, birds made up the largest proportion. Despite its small population in the region, willow grouse (*Lagopus lagopus*) was the most important prey species, both in numbers and body mass. The proportion of voles and lemmings (Microtinae sp), and that of smaller birds such as thrushes (*Turdus sp.*) in the diet was more important than expected from previous studies. No ungulates were delivered at the nest, which was in contrast to previous findings. The results found by Skouen (2012) was collected from only one pair of golden eagles, during one breeding season. Thus there is a need for more data from more nests.

I video monitored one nest of the rough-legged buzzard, and one nest of the golden eagle in Oppland county, southern Norway, in a peak vole year. The aims of my study were, to 1) analyse the diet composition, and evaluate the importance of microtine rodents in particular in the diet of both raptors, and the importance of ungulates in the diet of the golden eagle, and 2) investigate parental roles, nestling feeding-behavior and prey handling.

## MATERIALS AND METHODS

### STUDY SPECIES

The golden eagle is found throughout the northern hemisphere including the boreal region of Fennoscandia (Nyström et al. 2006; Rovdata 2014). As in most raptors, the golden eagles exhibit reversed sexual size dimorphism where the female is larger and heavier than the male (Newton 2010). The female has an average body mass of c. 5 kg, and the male c. 3.5 kg. Its wingspan measure 175 – 205 cm. It is a territorial bird, and can use the same territories and nesting sites for generations, within the territory there is often a few nesting sites to choose from (Hagen 1989; Watson 2010). The nests are typically placed on cliffs or in large pine trees in areas where human activity is limited (Watson 2010). The golden eagles start their breeding season in March-April when the eggs are laid, and incubation lasts for c. 43 days (Watson 2010). The Nestlings fledge when they are 70 - 80 days old. Usually only one of the young survives to fledge (Hagen 1989; Watson 2010).

Human influence on the golden eagle has been substantial, by both land use change and hunting. In 1968 the golden eagle was protected by law in Norway. At that time the Norwegian population probably reached the lowest densities in modern time with 300 - 500 nesting pairs. In 2008 the population was estimated to 1176-1454 nesting pairs (Gjershaug & Nygård 2003). The golden eagle has now been removed from the Norwegian Red List of threatened species (Artsdatabanken 2014).

The rough-legged buzzard has a circumpolar distribution in the northern hemisphere, and has a similar distribution in Norway as the golden eagle, but is more common further north and in subarctic areas (Gjershaug 1994). Its wingspan ranges from 120 - 140 cm. The rough-legged buzzard also exhibit reversed sexual size dimorphism and their body mass vary around 520-1370 g (Gjershaug 1994; Svensson et al. 2004). The rough-legged buzzard is a migratory bird that spend the winter months in central Europe. It nests are typically located on cliffs or in trees (Svensson et al. 2004). It arrives in Norway in March – April, and stay until September - October (Hagen 1989; Svensson et al. 2004). Eggs are laid in May, and incubation lasts c. 31 days. The nestlings fledge

30-40 days after hatching (Hagen 1989). The Norwegian population of rough-legged buzzards was estimated to be around 5000-10 000 breeding pairs in 1994, which was a peak vole year. Today it is listed as least concern at the Norwegian Red List of threatened species (Artsdatabanken 2014)

## STUDY AREA

The two nests studied were located in the boreal zone in Oppland County, south Norway c. 30 km apart. The exact location is excluded from public domain. The nest of the golden eagles was located on a cliff about 760 m above sea level. The surrounding forest is dominated by Norwegian spruce (*Picea abies*) intermixed with birch (*Betula sp.*). Willow (*Salix sp.*) and lush herb vegetation cover the ground (Rekdal 2002). From the nest site it is c. 3 km to the open alpine areas with bogs and lakes. Sheep graze in the area during summer (Skog og landskap 2015). It is estimated that there were about 55-65 breeding pairs of golden eagles in Oppland County in 2014, which is the highest number in recent years (Opheim & Høitomt 2014).

The nest of the rough-legged buzzards was situated on a cliff ledge at a slightly lower altitude (640 m above sea level) than the golden eagle nest. In an open forest landscape created by clear-cutting. The forest is dominated by Norwegian spruce, intermixed with birch and pine (*Pinus sylvestris*). Shrubs and willow herb (*Chamerion angustifolium*) cover the ground. The distance from the nest site to alpine areas is c. 4 km.

Observations indicate that the year 2014 was a year with very high densities of small mammals. Microtine rodents have been trapped annually at a site 50-100 km southeast of my study area in spring and fall since 1981. This trapping site is located the boreal forest c. 600 m above sea level. The number of microtinae rodents trapped in 2014 was the highest ever recorded (Geir A. Sonerud personal communication). It is thus reason to believe that voles and lemming were very abundant in my study area. Hunting bag statistics of small game from 2013 however, show a national decline and a historical low capture of grouse species and mountain hare, with the lowest recorded numbers since the surveillance started in the 1970`s (Nygård et al. 2013).

## VIDEO MONITORING

A small colour CCD (charge-couple device) camera was installed at the rough-legged buzzard nest and golden eagle nest during winter in 2013 and 2014, respectively. The cameras were positioned so as to have the best angle possible for observing the activity in the nest (Figure 1).



**Figure 1.** a) Still picture taken from the video recordings, captured at the golden eagle nest 23 May 2014 showing the male (front) having delivered a Norwegian lemming (*Lemmus lemmus*) to the nest, which is being fed to the nestling by the female. b) Still picture taken from the video recordings captured at the rough-legged buzzard nest 1 July 2014 showing female delivering a *Microtus* vole at the nest and feeding it to the three nestlings.

At both nests the camera was connected to a mini DVR (digital video recorder) by a c. 100 m long power and RCA video cable. The mini DVR that stored the recordings on a SD card was placed in a waterproof box along with a voltage converter two fuses (for details see Steen (2009)). A 12 V battery and a solar panel were used to power the system. The SD card was changed once a week, and at the same time an overall check that the technology was functioning sufficiently was made. To minimize disturbance caused by my visits, the box containing the recorder, and the battery was placed some distance from the nest.

The digital video monitoring system had a video motion detection sensor, so the recordings were triggered by movements at the nest. At each triggering, a video clip of up to seven s duration was recorded, and stored on an SD card. The sensitivity of the sensor was adjusted to a level which would capture all deliveries, but not be triggered by small movements, so the storage on the SD

card lasted about one week. To capture the inflight of the deliveries some area just outside the nest was included in the motion detection area.

The video monitoring was initiated 1 May at the golden eagle nest and 10 May at the rough-legged buzzard nest. The last visit to the nests was 12 July, when the SD card was exchanged for the last time and was set to record until it was full. For the golden eagle that turned out to be 22 July (82 days recorded), whereas for the rough-legged buzzard the video continued to record until 17 August (99 days recorded). The latter sustained for so long due to the buzzards leaving the nest around 20 July and after that only occasional movements from bugs or blowing branches in the nest activated the sensor. About 16 days' worth of recordings of was lost due to full SD cards. Altogether approximately 465 hours of video was recorded.

The two eggs hatched in the golden eagle nest 10-12 May, about a week after the monitoring started. One of the nestlings died 20 days after hatching, while the other survived to fledging. The video monitoring continued until the surviving nestling was 75 days and still had not left the nest. The six eggs in the rough-legged buzzard nest started to hatch 8 June. Two out of six eggs did not hatch, and one nestling died 12 days after hatching. The three remaining fledglings started leaving the nest sporadically and returning at 36 days after hatching, and at 41 days all the nestlings had left the nest.

## DATA PROCESSING

When browsing the recorded material I searched for any delivery of prey at the nest. Each prey delivered was assigned a category (mammal or bird), the date and time of day, the age of the nestlings at that day, the sex of the delivering parent, and whether the nestlings fed unassisted or was fed by the female. Morphological features such as relative size and plumage were used to determine the sex of the parent birds. The sections of recorded deliveries were put in folders and later analysed to identify the prey to the lowest taxonomic level possible. This prey identification was made with assistance from my supervisor. The video clips were projected on a 49" screen, and played frame by frame when necessary. When we were unable to identify the prey item to species level we looked at the relative size of the prey (comparing it to the delivering parent or nestling was helpful), or the relative tail length (for small mammals). For birds additional features

such as plumage and foot characteristics (if the foot had a hind claw, or if the tarsus was covered by feathers) was also used to determine the prey item to a more general group such as genus or family level. Some prey could only be determined to bird or small mammal.

A gross prey body mass was assigned to each prey item based on (Cramp & Perrins 1993 a; Cramp & Perrins 1993 b; Cramp & Perrins 1994 a; Cramp & Perrins 1994 b; Frislid & Jensen 2004). A net body mass was estimated if the prey item was not intact at the delivery. If the prey item was decapitated I subtracted 20 % for large mammalian prey such as European pine marten (*Martes martes*) and mountain hare. For a decapitated vole or lemming 16.5 % was subtracted (Asakskogen 2003) and for decapitated birds 12.9 % of the total prey mass was subtracted when decapitated (T. Slagsvold & G. A. Sonerud, unpublished data). When other parts of the prey were missing an estimate of the body mass was made by my supervisors.

The weather data was extracted from the nearest meteorological stations. The database eKlima (2015) provided information from Gausdal- Follebu 13030 and Fåvang 13150 meteorological stations which were the closest stations with sufficient number of loggings per day. These stations logged the ambient temperature four times a day. The ambient temperature at each delivery was interpolated linearly from the nearest temperature logging before and after the delivery. Precipitation was only logged on a daily basis, so all prey items delivered on the same day was given the same value for precipitation.

## STATISTICAL ANALYSES

Statistical analyses were performed with the software JMP® Pro 10.0.0. Standard criterion of statistical significance was  $< 0.05$ . Logistic regression was used to test for significant effects of different explanatory variables on a response variable. Variables were prey type, age of the nestlings, gross prey body mass, whether the male or the female delivered the prey, whether the delivery was made before or after midday, whether the nestling fed unassisted or was fed by the female, the time from midday (midday was set at 13.21 hours for the rough-legged buzzard nest, and at 13.20 hours for the golden eagle nest), ambient temperature and precipitation. For the analyses of the golden eagle the following additional categories for ways of grouping the prey type

variable were Norwegian lemming or other prey, Norwegian lemming or other mammal, Norwegian lemming or other microtines, microtines or other prey, microtines or other mammal, thrush (*Turdus sp.*) or other prey, thrush (*Turdus sp.*) or other bird, grouse (Tetraonidae sp.) or other prey, and grouse (Tetraonidae sp.) or other bird. For the prey items delivered with missing parts net prey body mass was used. The net prey body mass was only used in the golden eagle analyses, due to difficulty in determining if the prey item was decapitated or not when delivered at the rough-legged buzzard nest. Variables were excluded by likelihood ratio test until only significant variables remained. The parameter estimates and associated  $p$  values from Wald test are presented in the results. Logistic fit and contingency tables were used to visualize the significant values. Mean values are given with one standard error.

## RESULTS

### THE DIET OF THE GOLDEN EAGLE

During the monitoring period, the breeding pair of golden eagles delivered 120 prey items at the nest (Table 1). Of these items 65 were determined to species level, 49 to genus level and 6 to family level. There was a greater number of mammals than birds delivered at the nest, respectively 66 % and 34 %. In terms of body mass the mammals also dominated, with 73 % of the total gross body mass delivered at the nest. The prey species that made up the largest mass in total was mountain hare, with 62 % of the net body mass delivered to the nest, and 65 % of the total gross body mass of delivered items. Mountain hare was therefore the most important food resource for the breeding pair of golden eagles. Of all the prey delivered 51 % were microtine rodents, the majority being Norwegian lemming (29 % of total and 68 % of the microtine rodents). Norwegian lemming was the most numerous prey species delivered. Of the birds delivered, unidentified species of thrush (*Turdus sp.*) were the most numerous, but species of grouse (Tetraonidae sp.) especially ptarmigan (*Lagopus sp.*) and capercaillie (*Tetrao urogallus*) were more important in terms of body mass. Together with black grouse (*Tetrao tetrix*) these species of grouse made up 22 % of the estimated gross body mass delivered at the nest. No ungulate was recorded delivered at the nest during the period of video monitoring.



**Table 1.** Prey items delivered at the golden eagle nest during the monitoring period (1 May – 22 July 2014). The percentages are given for the number of prey and for estimated net and gross body mass of prey items delivered.

Prey type	Prey number		Prey mass			
	N	%	Estimated body mass (g) net	Estimated body mass (g) gross	% of total estimated mass (net)	% of total estimated mass (gross)
<b>Mammal</b>						
Norwegian lemming ( <i>Lemmus lemmus</i> )	35	29.2	50 <sup>1</sup>	50	3.5	2.4
Wood lemming ( <i>Myopus schisticolor</i> )	1	0.8	30	30	0.06	0.04
Red-backed vole ( <i>Myodes</i> sp.)	1	0.8	40	40	0.08	0.05
Field vole or Root vole ( <i>Microtus</i> sp.)	17	14.2	50 <sup>2</sup>	50	1.7	1.2
Vole indet. ( <i>Microtinae</i> sp.)	7	5.8	43 <sup>3</sup>	50	0.6	0.5
Mountain hare ( <i>Lepus timidus</i> )	16	13.3	1963 <sup>4</sup>	3000	62.1	65.8
European pine marten ( <i>Martes martes</i> )	2	1.7	1200	1200	4.8	3.3
<i>Total mammal</i>	79	65.8			72.8	73.2
<b>Bird</b>						
Capercaillie ( <i>Tetrao urogallus</i> )	5	4.2	950 <sup>5</sup>	2000	9.4	13.7
Black grouse ( <i>Tetrao tetrix</i> )	2	1.7	1150 <sup>6</sup>	1300	4.5	3.6
Willow ptarmigan ( <i>Lagopus lagopus</i> )	1	0.8	500	500	1	0.7
Ptarmigan indet. ( <i>Lagopus</i> sp.)	6	5.0	500	500	5.9	4.1
Wood sandpiper ( <i>Tringa glareola</i> )	1	0.8	60	60	0.1	0.08
Eurasian teal ( <i>Anas crecca</i> )	1	0.8	300	300	0.6	0.4
Duck indet. (Anatidae)	5	4.2	180 <sup>7</sup>	200	1.8	1.4
Thrush indet. ( <i>Turdus</i> sp.)	19	15.8	95 <sup>8</sup>	100	3.6	2.6
Hawk indet. (Accipitridae)	1	0.8	200	200	0.4	0.3
<i>Total bird</i>	41	34.2			27.3	26.9
<b>Total</b>	<b>120</b>	<b>100.0</b>			<b>100.0</b>	<b>100.0</b>

<sup>1</sup> Mean estimate, variation 40-50 g

<sup>2</sup> Mean estimate, variation 40-50 g

<sup>3</sup> Mean estimate, variation 40-50 g

<sup>4</sup> Mean estimate, variation 500-3000 g

<sup>5</sup> Mean estimate, variation 50-2000 g

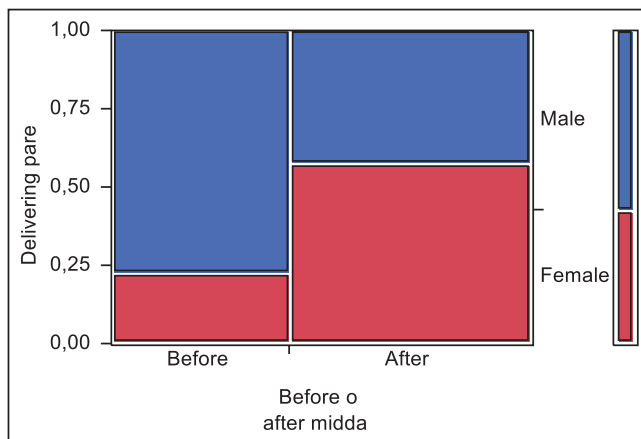
<sup>6</sup> Mean estimate, variation 1000-1300 g

<sup>7</sup> Mean estimate, variation 100-200 g

<sup>8</sup> Mean estimate, variation 50-100 g

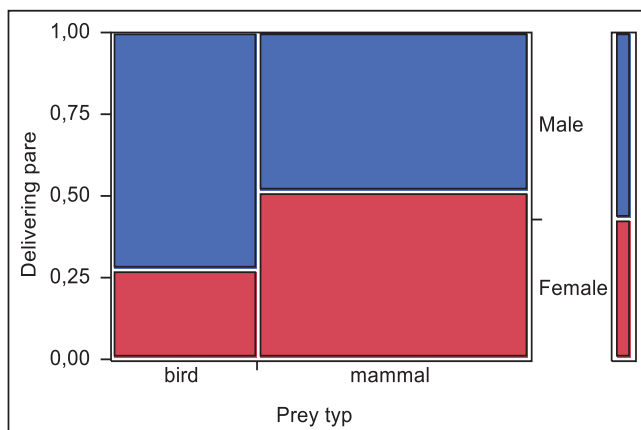
## DELIVERING PARENT

The male made the majority of the deliveries at the nest (57 %). The larger part of deliveries took place after midday (58 %). The probability that a prey item was delivered by the male was significantly affected by time of day at delivery (Table 2). A prey item was more likely to be delivered by the male when it was delivered before midday, than when it was delivered after midday (Figure 2).



**Figure 2.** The distribution of the delivering sex (male or female) on the time (before or after midday) the prey was delivered at the golden eagle nest. Whole model:  $N = 115$ ,  $\chi^2 = 14.74$ ,  $df = 1$ ,  $p < 0.0001$

The probability that the prey was delivered by the male was also significantly affected by the type of prey (bird or mammal) delivered at the nest (Table 2). The probability that a prey item was delivered by the male was significantly higher for birds than for mammals (Figure 3).

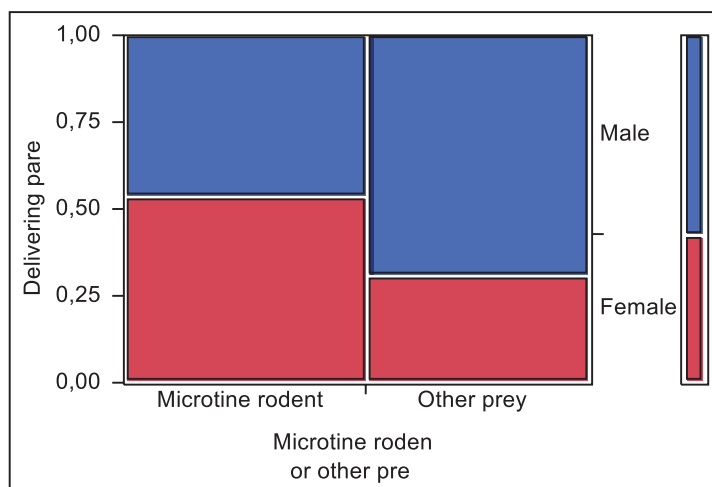


**Figure 3.** The distribution of the delivering sex (male or female) on prey type (bird or mammal) delivered at the golden eagle nest. Whole model.  $N = 115$ ,  $\chi^2 = 6.20$ ,  $df = 1$ ,  $p = 0.013$

**Table 2.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression with sex of the delivering parent at the golden eagle nest as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 114$ ,  $\chi^2 = 22.66$ ,  $df = 2$ ,  $p < 0.0001$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-0.663	0.239		7.70	0.0055
Before or after midday	0.849	0.222	1	14.58	0.0001
Prey type (bird or mammal)	-0.598	0.230	1	6.78	0.0092

Approximately half of the delivered prey items was a microtine rodent (51%). The probability that the prey was delivered by the female was significantly affected by whether the prey was a microtine rodent or other prey (Table 3). The female was more likely than the male to deliver a microtine rodent rather than another prey (Figure 4).



**Figure 4.** The distribution of the delivering sex (male or female) on whether a microtine rodent rather than another prey was delivered to the golden eagle nest. Whole model:  $N = 115$ ,  $\chi^2 = 5.97$ ,  $df = 1$ ,  $p = 0.015$

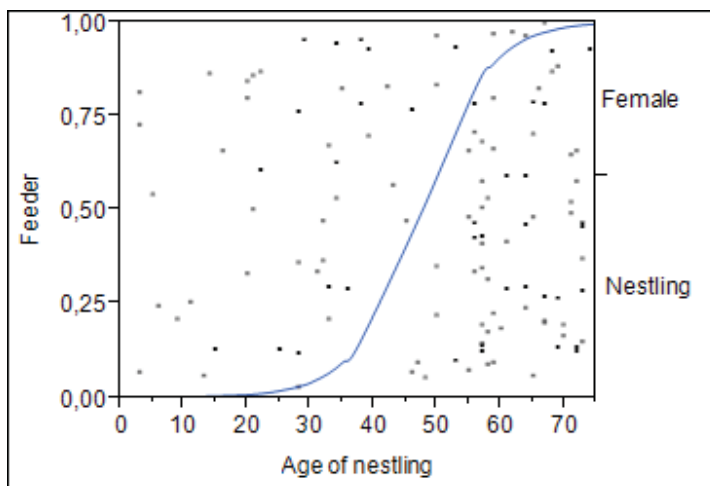
When the prey delivered variable was defined as microtine rodent or other prey, the probability that the prey was delivered by the male was once more significantly affected by the time of day (before or after midday) the prey item was delivered at the nest (Table 3). The probability that a prey item was delivered by the male was significantly higher before midday than after (Figure 2).

**Table 3.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression with delivering parent at the golden eagle nest as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 115$ ,  $\chi^2 = 20.44$ ,  $df = 2$ ,  $p < 0.0001$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-0.509	0.219		5.43	0.020
Before or after midday	0.787	0.218	1	13.03	0.0003
Microtine rodent or other prey	0.490	0.209	1	5.50	0.019

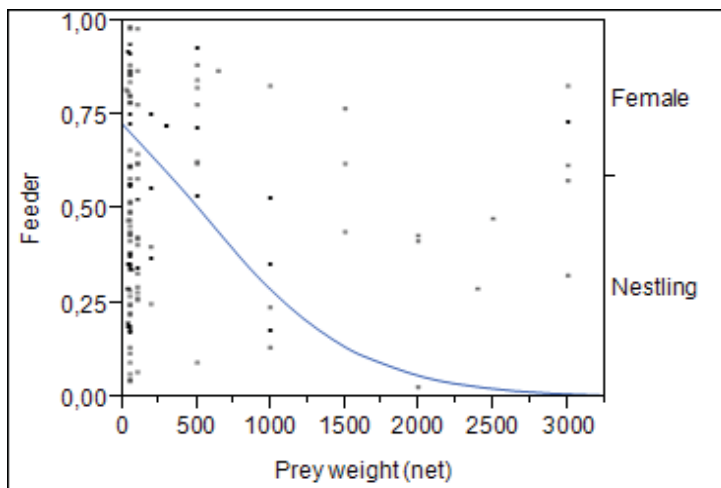
## PREY HANDLING

The nestling was recorded feeding unassisted for the first time 28 days after hatching. The female was the only parent feeding, and the nestling fed unassisted for the majority of the prey (59 %). The probability that the nestling fed unassisted significantly increased as the nestling became older (Table 4, Figure 5).



**Figure 5.** The probability that the golden eagle nestling fed unassisted as a function of age of the nestling (days). Whole model:  $N = 119$ ,  $\chi^2 = 99.71$ ,  $df = 1$ ,  $p < 0.0001$ .

The predicted age at which the nestling was as likely to feed unassisted, as to be fed by the female, was 47 days after hatching (Figure 5). The net prey body mass significantly affected the probability that the nestling fed unassisted independent of nestling age (Table 4). If the prey item delivered was small, it was more likely that the nestling fed unassisted (Figure 6).



**Figure 6.** The probability that the nestling fed unassisted as a function of the net body mass (g) of the prey delivered to the golden eagle nest. Whole model:  $N=119$ ,  $\chi^2=25.19$ ,  $df=1$ ,  $p<0.0001$

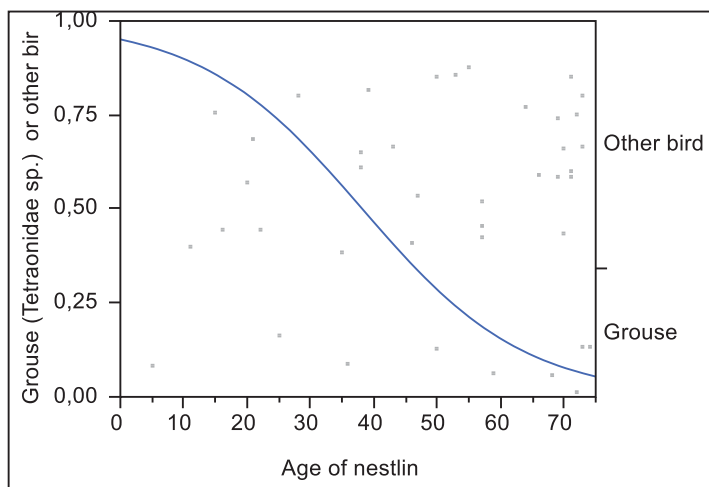
The mean net body mass of all the prey items delivered at the nest was  $422 \text{ g} \pm 70 \text{ g}$ . The mean estimated gross body mass of all prey items delivered was  $607 \text{ g} \pm 94 \text{ g}$ .

**Table 4.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression with whether the female golden eagle fed or the nestling fed unassisted as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N=119$ ,  $\chi^2=126.26$ ,  $df=2$ .  $p<0.0001$

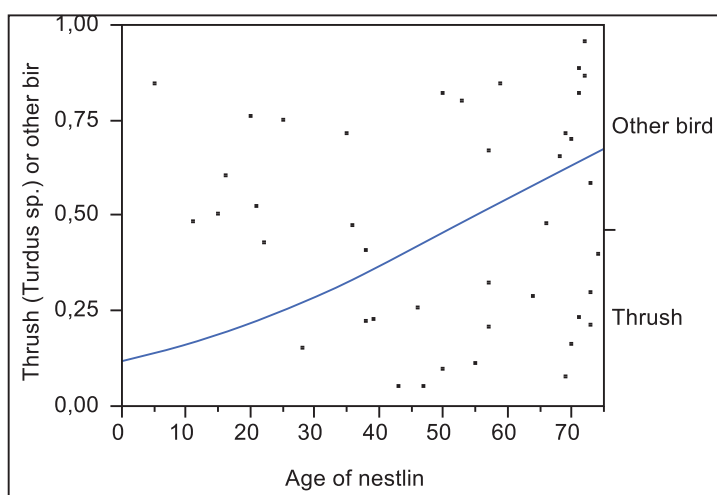
Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	10.058	2.311		18.94	< 0.0001
Prey body mass (net)	0.004	0.001	1	10.56	0.0012
Age of nestling	-0.237	0.050	1	22.95	< 0.0001

## SELECTION OF THRUSHES AND GROUSE AS PREY

The probability that the prey delivered at the nest was a grouse (*Tetraonidae* sp.) rather than other bird (Table 5), and a thrush (*Turdus* sp.) rather than another bird (Table 6), was significantly affected by the age of the nestling. The probability that a grouse (*Tetraonidae* sp.) rather than another bird was delivered at the nest was higher earlier in the season (Figure 7), and the probability that a thrush (*Turdus* sp.) rather than another bird was delivered at the nest was higher later in the season (Figure 8).



**Figure 7.** The probability that a bird delivered at golden eagle nest was a grouse (*Tetraonidae* sp.) rather than another bird as a function of age of nestling (days). Whole model:  $N = 41$ ,  $\chi^2 = 16.54$ ,  $df = 1$ ,  $p < 0.0001$



**Figure 8.** The probability that a bird delivered at the golden eagle nest was a thrush (*Turdus* sp.) rather than another bird as a function of age of nestling (days). Whole model:  $N = 41$ ,  $\chi^2 = 16.54$ ,  $df = 1$ ,  $p < 0.0001$

**Table 5.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with whether a grouse (*Tetraonidae* sp.) rather than another bird was delivered to the golden eagle nest as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 41$ ,  $\chi^2 = 16.54$ ,  $df = 1$ ,  $p = <0.0001$

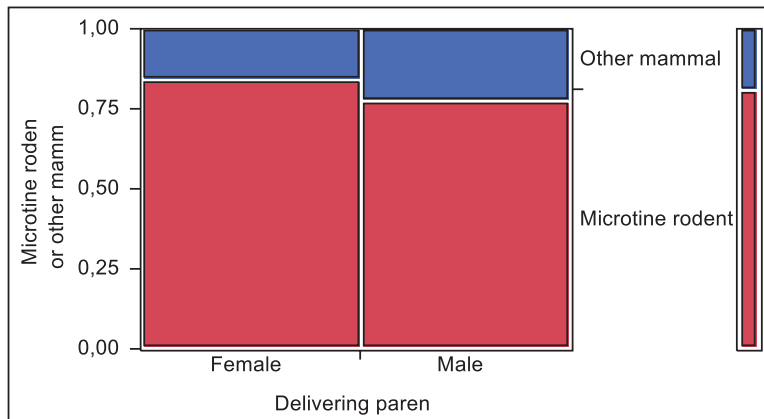
Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-2.968	1.140		6.78	0.0092
Age of nestling	0.078	0.024	1	10.76	0.0010

**Table 6.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with thrush (*Turdus* sp.) or other bird as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 41$ ,  $\chi^2 = 4.99$ ,  $df = 1$ ,  $p = <0.026$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	2.011	0.978		4.23	0.040
Age of nestling	-0.037	0.018	1	4.33	0.037

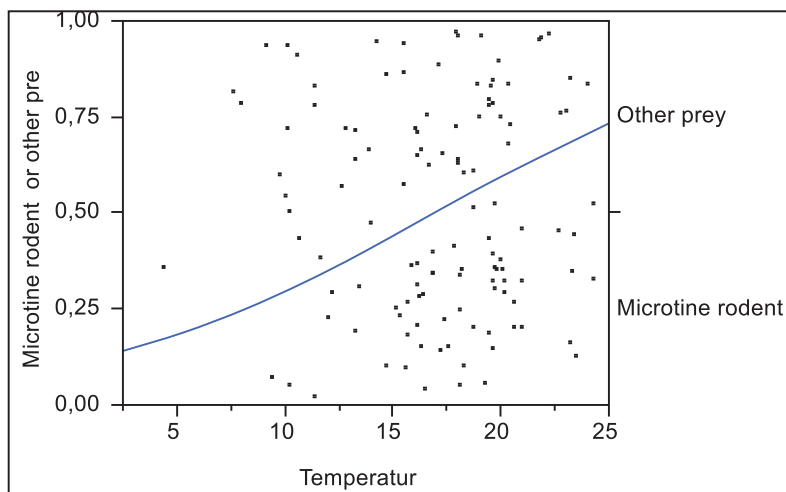
## SELECTION OF MICROTINE RODENTS AS PREY

The probability that the prey delivered was a microtine rodent rather than another prey was significantly affected by the sex of the delivering parent (Table 7). The probability that the prey item delivered was a microtine rodent was significantly higher when the female delivered the prey than when the male delivered the prey (Figure 9).



**Figure 9.** The distribution of whether a microtine rodent rather than another prey was delivered at the golden eagle nest on the sex of the delivering parent (male or female). Whole model:  $N=115$   $\chi^2 = 5.97$ ,  $df = 1$ ,  $p = 0.015$

The probability that the prey delivered at the nest was a microtine rodent rather than another prey increased with increasing ambient temperature (Table 7, Figure 10).



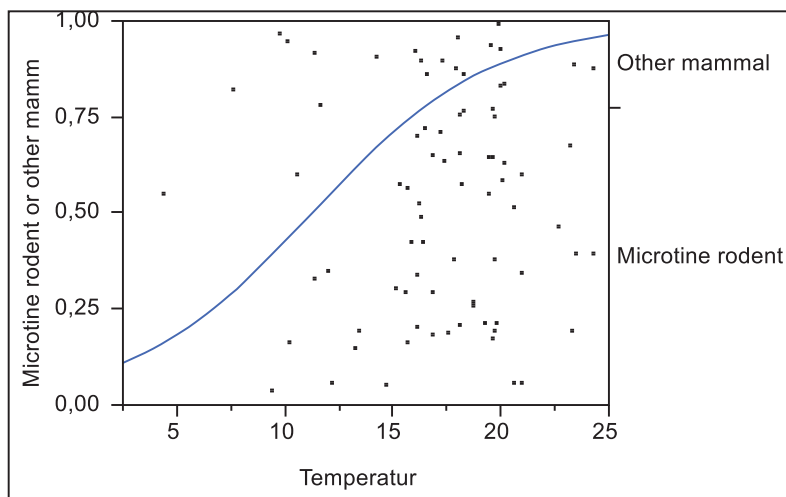
**Figure 10.** The probability that prey brought to the golden eagle nest was a microtine rodent rather than another prey as a function of ambient temperature (°C). Whole model:  $N = 120$ ,  $\chi^2 = 7.11$ ,  $df = 1$ ,  $p = 0.0077$



**Table 7.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with whether a microtine rodent rather than another prey was delivered at the nest of the golden eagles as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 115$ ,  $\chi^2 = 11.04$ ,  $df = 2$ ,  $p = 0.004$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-1.810	0.931		3.79	0.051
Delivering parent (male or female)	0.438	0.199	1	4.84	0.028
Temperature	0.114	0.052	1	4.74	0.03

The probability that the prey item delivered at the nest was a microtine rodent rather than another mammal was also significantly affected by ambient temperature (Table 8). When the ambient temperature increased there was a higher probability that the prey delivered at the nest was a microtine rodent rather than another mammal (Table 8, Figure 11).



**Figure 11.** The probability that the prey delivered at the golden eagle nest was a microtine rodent rather than another mammal as a function of ambient temperature ( $^{\circ}\text{C}$ ). Whole model:  $N = 79$ ,  $\chi^2 = 11.38$ ,  $df = 1$ ,  $p = 0.0007$

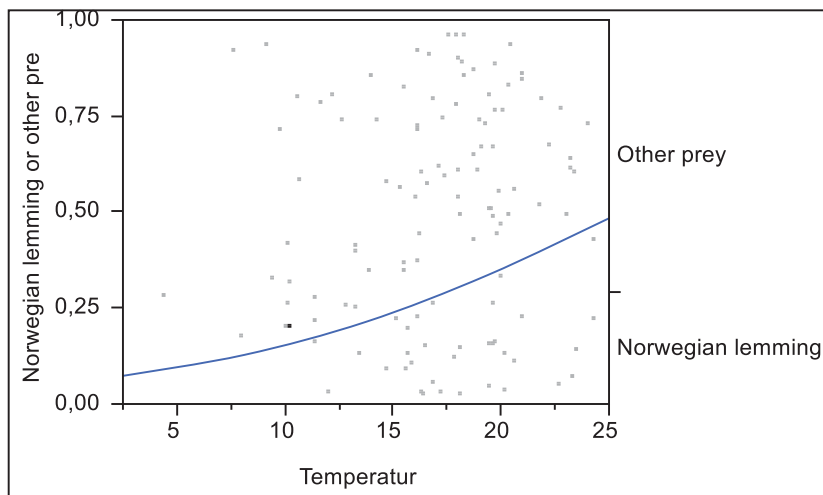
The mean ambient temperature at the deliveries was  $17^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$ , and the mean precipitation was  $2.3 \text{ mm} \pm 0.6 \text{ mm}$  per day during the monitoring period. Precipitation was not a significant ( $p = 0.059$ ) variable but showed a tendency that a microtine rodent was more likely to be delivered at the nest during rainfall than other mammals.

**Table 8.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with whether a microtine rodent rather than another mammal was delivered at the golden eagle nest as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 79$ ,  $\chi^2 = 11.38$ ,  $df = 1$ ,  $p = 0.0007$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-2.693	1.260		4.56	0.033
Temperature	0.239	0.077	1	9.49	0.0021

## SELECTION OF NORWEGIAN LEMMING AS PREY

The Norwegian lemming was the most numerous prey delivered to the nest. The probability that the prey delivered at the nest was a Norwegian lemming rather than another prey was significantly affected by ambient temperature (Table 9). The probability that the prey delivered was a Norwegian lemming increased with higher ambient temperature (Figure 12).



**Figure 12.** The probability that the prey delivered at to the golden eagle nest was a Norwegian lemming rather than another prey, as a function of ambient temperature ( $^{\circ}\text{C}$ ). Whole model:  $N = 120$ ,  $\chi^2 = 4.34$ ,  $df = 1$ ,  $p = 0.038$ .

**Table 9.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with whether a Norwegian lemming rather than another prey was delivered at the golden eagle nest as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 120$ ,  $\chi^2 = 4.33$ ,  $df = 1$ ,  $p = 0.038$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-2.812	1.001		7.88	0.005
Temperature	0.110	0.055	1	3.97	0.046

Whether a Norwegian lemming or other microtine rodent was delivered at the nest was also significantly affected by the interaction between precipitation and the age of the nestling (Table 10). Precipitation and age of the nestling was not significant in itself, however they showed a tendency that the probability of a lemming rather than other species of microtine rodent being delivered to the nest increased during rainfall and throughout the season.

**Table 10.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression with whether a Norwegian lemming rather than another microtine rodent as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 59$ ,  $\chi^2 = 7.24$ ,  $df = 3$ ,  $p = 0.065$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-1.154	1.262		0.84	0.36
Precipitation	-0.117	0.087	1	1.81	0.18
Age of nestling	0.035	0.025	1	1.95	0.16
Precipitation*Age of nestling	0.010	0.008	1	1.40	0.24

## THE DIET OF THE ROUGH-LEGGED BUZZARD

Altogether 253 prey items were delivered at the nest of the breeding pair of rough-legged buzzard during the monitoring period (Table 11). Of these six items were determined to species level, 231 to genus level, seven to family level, and nine could only be determined to prey type (bird or mammal). Mammals made up 90 % of the delivered prey brought to the nest, and 84 % of the total estimated body mass delivered. The majority (94 %) of the mammals delivered were microtine rodents. The most common prey genus was *Microtus* voles (field vole (*Microtus agrestis*) or root vole (*Microtus oeconomus*)), which made up 71 % of the deliveries and 69% of the total estimated body mass. This made *Microtus* voles the most important food resource both in body mass and in numbers. Undetermined species of thrushes (*Turdus sp.*) made up the majority of birds delivered at the nest, with 8 % of total prey delivered and 15 % of the total estimated body mass. The remaining birds delivered at the nest were unidentified passerines, which accounted for 3 % of the prey items delivered

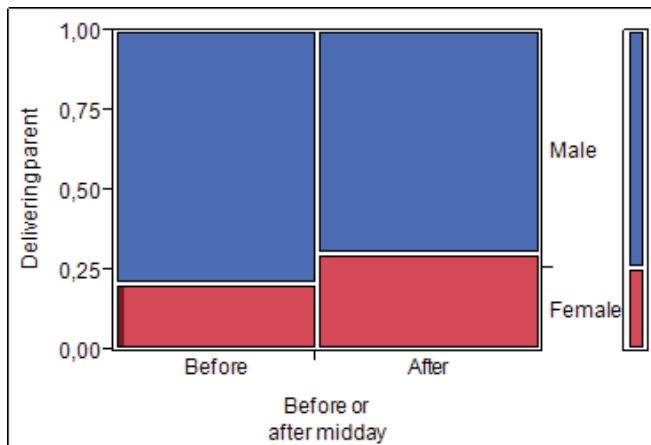
**Table 11.** Prey items delivered at the rough-legged buzzard nest during the monitoring period (10 May – 17 August 2014). The percentages are given for the number of prey and estimated gross body mass.

Prey type	Prey number		Prey mass	
	N	%	Estimated body mass (g)	% of total estimated mass
<b>Mammals</b>				
Water vole ( <i>Arvicola amphibius</i> )	3	1	100	2.3
Norwegian lemming ( <i>Lemmus lemmus</i> )	1	0.4	50	0.4
Red-backed vole ( <i>Myodes sp.</i> )	2	0.8	30	0.5
Field vole or Root vole ( <i>Microtus sp.</i> )	179	71	50	69
Vole indet. ( <i>Microtinae sp.</i> )	28	11	40	8.6
Shrew ( <i>Soricidae sp.</i> )	5	2	10	0.4
Small mammal indet.	9	4	40	2.8
<i>Total mammals</i>	<i>227</i>	<i>89.7</i>		<i>83.9</i>
<b>Birds</b>				
Thrush indet. ( <i>Turdus sp.</i> )	19	7.5	100	14.6
Passerine indet. (Passeriformes)	7	2.8	27 <sup>9</sup>	1.5
<i>Total birds</i>	<i>26</i>	<i>10.3</i>		<i>16.1</i>
<b>Total</b>	<b>253</b>	<b>100.0</b>		<b>100.0</b>

<sup>9</sup> Mean estimate, variation 20-70 g

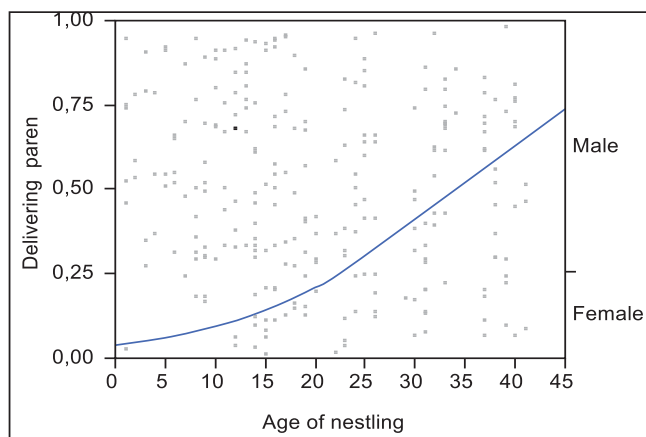
## DELIVERING PARENT

The male rough-legged buzzard made the majority of the prey deliveries at the nest (75 %). Slightly more prey was delivered at the nest after midday (52 %) than before midday. The probability that a prey was delivered by the male was significantly affected by whether the prey was delivered before or after midday (Table 12). The male was significantly more likely to deliver a prey item at the nest before than after midday (Figure 14).



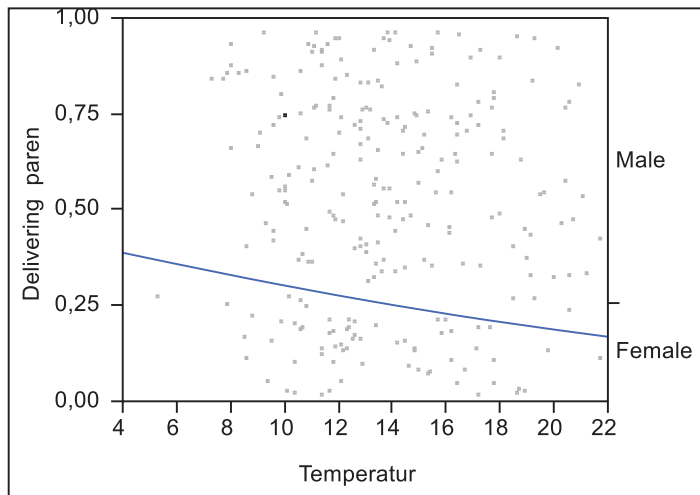
**Figure 14.** The distribution of the delivering sex (male or female), on the time of prey delivery (before or after midday) at the rough-legged buzzard nest. Whole model:  $N = 253$ ,  $\chi^2 = 2.97$ ,  $df = 1$ ,  $p = 0.085$ .

The probability that the male was the delivering parent was significantly affected by the age of the nestlings (Table 12). As the nestlings become older the male was less likely to be the delivering parent (Figure 15). The predicted age of the nestlings when the male and the female was as likely to deliver a prey item at the nest was 34 days (Figure 15).



**Figure 15.** The probability that the female rough-legged buzzard was the delivering parent as a function of the age of the nestlings (days). Whole model:  $N = 253$ ,  $\chi^2 = 44.79$ ,  $df = 1$ ,  $p < 0.0001$ .

The probability that the male was the delivering parent was significantly affected by ambient temperature (Table 12). With increasing ambient temperature, it was more likely that the male was the delivering parent (Figure 16). The mean ambient temperature at the deliveries was  $13.4^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$ .



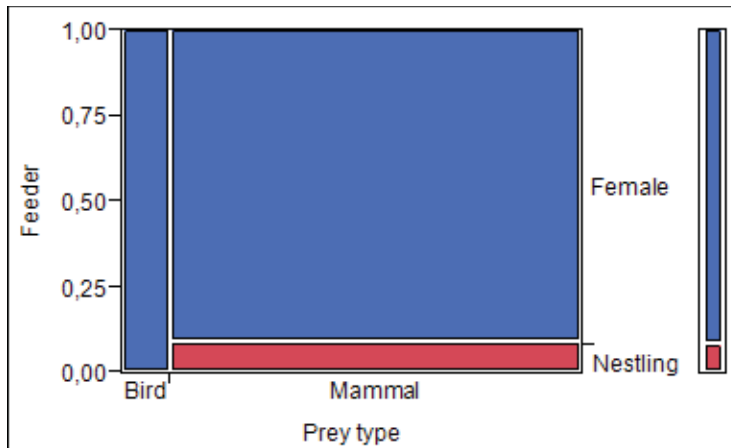
**Figure 16.** The probability that the female rough-legged buzzard delivered was the delivering parent as a function of ambient temperature ( $^{\circ}\text{C}$ ). Whole model:  $N = 253$ ,  $\chi^2 = 2.13$ ,  $df = 1$ ,  $p = 0.14$ .

**Table 12.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with delivering parent as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test): Whole model:  $N = 253$ ,  $\chi^2 = 63.86$ ,  $df = 3$ ,  $p < 0.0001$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-0.912	0.750		1.48	0.22
Before or after midday	0.565	0.182	1	9.64	0.0019
Temperature	-0.223	0.062	1	12.86	0.0003
Age of nestlings	0.122	0.019	1	39.64	< 0.0001

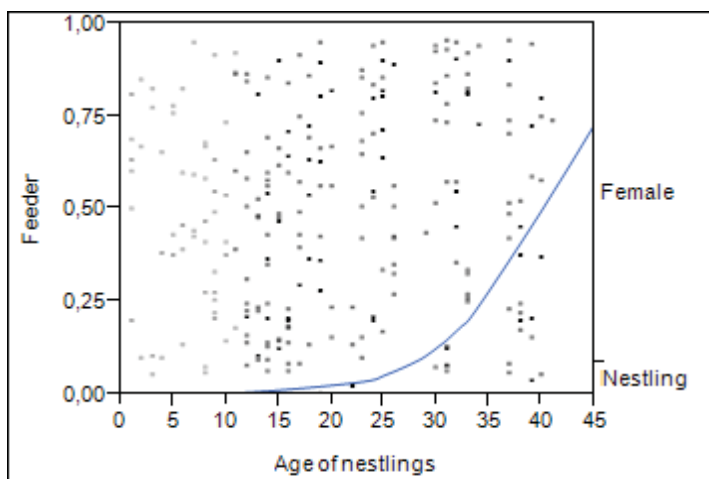
## PREY HANDLING

The feeding parent was exclusively the female. For 92 % of the delivered prey she was the one feeding and she did so until the nestlings left the nest. For the remaining 8 % of the prey the nestlings fed unassisted. The probability that the nestlings would feed unassisted was higher when the prey delivered was a mammal than when it was a bird (Table 13, Figure 17).



**Figure 17.** The distribution of whether the female fed or the nestlings fed unassisted, on the prey type (bird or mammal) that was delivered at the rough-legged buzzard nest. Whole model:  $N = 249$ ,  $\chi^2 = 4.85$ ,  $df = 1$ ,  $p < 0.028$ .

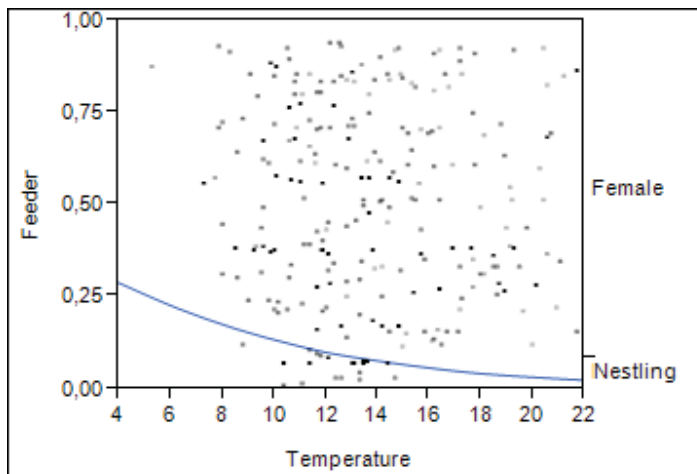
The probability that the nestlings would feed unassisted was significantly affected by the age of the nestlings (Table 13). As the nestlings became older, they were more likely to feed unassisted (Figure 18). The predicted age at which the nestlings were as likely to feed unassisted as to be fed by the female was 40 days (Figure 18).



**Figure 18.** The probability that the rough-legged buzzard nestlings fed unassisted, as a function of age of the nestlings (days). Whole model:  $N = 250$ ,  $\chi^2 = 47.44$ ,  $df = 1$ ,  $p < 0.0001$ .

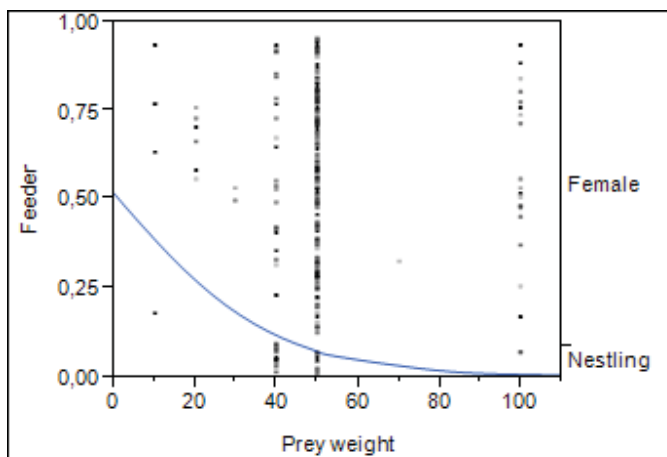


Ambient temperature significantly affected whether the female fed the nestlings or the nestlings fed unassisted (Table 13). The probability that the nestlings would feed unassisted decreased with increasing ambient temperature (Figure 19).



**Figure 19.** The probability that the rough-legged buzzard nestling fed unassisted as a function of ambient temperature (°C). Whole model:  $N = 250$ ,  $\chi^2 = 5$ ,  $df = 1$ ,  $p = 0.025$ .

The body mass of the prey item delivered at the nest also significantly affected the probability that the nestlings fed unassisted (Table 13). The probability that the nestlings fed unassisted significantly increased with decreasing size of the prey delivered at the nest (Figure 20).



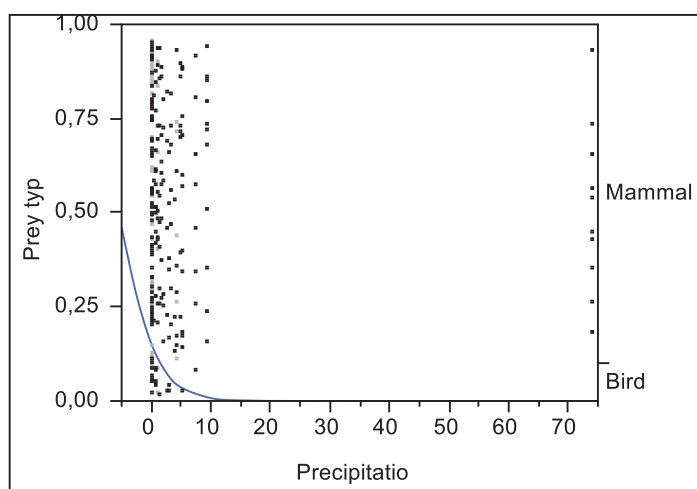
**Figure 20.** The probability that the rough-legged buzzard nestlings would feed unassisted as a function of prey body mass (g). Whole model:  $N = 250$ ,  $\chi^2 = 9.20$ ,  $df = 1$ ,  $p = 0.0024$ .

**Table 13.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with whether the female rough-legged buzzard fed the nestlings, rather than the nestlings fed unassisted as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 249$ ,  $\chi^2 = 85.41$ ,  $df = 4$ ,  $p < 0.0001$

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-5.180	2417.844		<0.01	0.99
Temperature	-0.743	0.202	1	13.49	0.0002
Age of nestlings	0.332	0.070	1	22.50	< 0.0001
Prey body mass	-0.152	0.040	1	14.85	0.0009
Prey type	-9.634	2417.844	1	<0.01	0.99

## EFFECTS OF PRECIPITATION ON PREY SELECTION

The probability that the prey delivered at the nest was a bird or a mammal was significantly affected by precipitation (Table 15). The probability that a bird was delivered decreased with increasing rainfall (Figure 26). The mean daily precipitation in the period of monitoring was  $0.6 \text{ mm} \pm 0.9 \text{ mm}$ .



**Figure 20.** The probability that a bird or mammal was delivered at the nest as a function of precipitation. Whole model:  $N = 253$ ,  $\chi^2 = 9.88$ ,  $df = 1$ ,  $p = 0.0017$ .

**Table 14.** Final model from backward elimination of variables based on likelihood ratio tests in a logistic regression model with prey type (bird or mammal) as response variable. Parameter estimates for the given variables are from Wald test. Whole model (log likelihood ratio test):  $N = 253$ ,  $\chi^2 = 9.88$ ,  $df = 1$ ,  $p = 0.0017$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-1.722	0.240		51.37	< 0.0001
Precipitation	-0.313	0.143	1	4.82	0.028

## DISCUSSION

My results are based on data from only one nest of the golden eagle and one nest of the rough-legged buzzard, and are thus too small for general conclusions. Of the 120 prey items recorded delivered at the golden eagle nest mammals were more abundant than birds, and mammals were also more important in terms of mass. The main prey item in the diet by mass was the mountain hare, which made up 66 %, followed by respectively capercaillie (14 %), ptarmigan (5 %) and black grouse (4 %). Together these prey made up 89 % of the total gross body mass in the recorded diet. The dominance of these prey species is typical for the golden eagles in Fennoscandia (Tjernberg 1981; Sulkava et al. 1999; Nyström et al. 2006; Moss et al. 2012). There was a surprisingly large proportion of Norway lemming and voles delivered at the nest. Norwegian lemmings was the most numerous prey species delivered at the nest, and together with other species of microtine rodents, it counted for half of the delivered prey at the nest. In the year of my study there were extremely high densities of microtine rodents.

High densities of microtine rodents have previously been related to the breeding success of golden eagles. Tjernberg (1983) investigated the reproductive performance of the golden eagle in northern Sweden in relation to densities of its primary prey (mountain hare and grouse (*Tetraonidae* sp.)) and microtine cycles. Based on data from 1975-1980 (Tjernberg 1983) predicted that the reproductive performance of golden eagles should vary in relation to the 3–4-year cycles showed by voles and not in the cycles shown by its primary prey. The golden eagle population would thus display a reproductive peak of one year after a vole peak. Moss et al. (2012) wanted to further explore Tjernberg (1983) predictions in a large scale study. The golden eagle reproduction was tested over a 30-yrs study period was related to both the primary small game prey, and to the vole abundance the previous autumn. Just as Tjernberg (1983) had found, Moss et al. (2012) found that vole abundance the previous autumn explained almost as much of the variation in the index of annual population production as the indices of primary prey did in the current year. Moss et al. (2012) considered this a result of the high densities of voles acting as a buffer to protect small game against predation by other predators, and thus increase the overwinter survival of the small game, that is the primary prey of the eagles. Moss et al. (2012) argued that it was unlikely that the golden eagle would switch to voles when these were abundant and that this could directly lead to

a higher breeding success the following year. I argue that the large proportion of voles and lemmings found in my study suggests that golden eagles respond functionally to voles and lemmings when they are abundant, and that voles and lemmings may affect reproduction success of golden eagles directly.

Further support for this idea can be found in another Swedish study. Analyses of prey remains and pellets in a study by Nyström et al. (2006) showed a large proportion of voles and Norway lemming in the diet of a golden eagle population in the Swedish mountain tundra. Nyström et al. (2006) studied the diet of golden eagles and the relationship between prey density fluctuations and breeding success of a golden eagle population in the mountain tundra region of northern Sweden. Microtine rodents made up 11 % of the diet. More than half of the microtine rodent remains were found during the 2001 season which was a peak year in the microtine cycle. Nyström et al. (2006) therefore suggested that the eagles responded functionally to voles and lemmings when they reached high densities.

The majority of the microtine rodent found in the nests in Nyström et al. (2006) was Norwegian lemmings despite that the densities of grey sided voles (*Myodes rufocanus*) were higher. This indicated a possible preference for Norwegian lemmings, or that the colouration of the lemmings made them easier to discover and their lesser mobility than grey-sided voles made them easier to capture. I regard all these valid explanations for why lemmings were taken in such large numbers also in my study. In addition, my analyses showed that the probability that a Norwegian lemming was taken, rather than another microtine rodent increased towards the end of the monitoring period, but only during rainfall. This may indicate that the high reproductive output of lemmings made them more available later in the season when they may have reached high densities. Furthermore, lemmings are more active relative to other rodents in rainy weather, in addition to them being more easy to discover in rainy weather compared to other microtine rodent due to its aposematic colouration (Andersson 2015). Most diurnal birds have an advanced colour vision (Honkavaara et al. 2002). There is thus reason to believe that the colours of a Norwegian lemming are just as visible to eagles as to humans (Andersson 2015).

Based on video recordings, also Skouen (2012) concluded that Norwegian lemming and voles were important prey of the golden eagle both in numbers, and connected it to findings of Slagsvold and

Sonerud (2007) that small prey are more profitable than large prey. Thus, golden eagles included small prey items in their diet to such a large degree, because these prey can be ingested at a higher rate than large prey and are therefore an important prey in the breeding diet.

The fact that Skouen (2012) and I used video monitoring to assess the diet can explain the large proportion of small prey present in the diet compared to other studies using traditional methods. These methods are known to be biased and underestimate small prey and overestimate large prey, which can lead to a misinterpretation of the diet (Lewis et al. 2004; Tornberg & Reif 2007). Selås et al. (2007) found for common buzzards (*Buteo buteo*) in Norway that voles and small mammals were underestimated, and birds overestimated when comparing remains and pellets with video recordings made at the nest. While watching the recordings I frequently observed removal of remains from larger prey, and direct ingestion of smaller mammals by the nestling, leaving no remains.

The lack of ungulates in the diet of the golden eagle in my study also contrasted from most studies made on the golden eagle diet. Previous studies has estimated that up to 11 % of the golden eagle diet is made up of reindeer (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007; Sánchez-Zapata et al. 2010; Watson 2010), and the golden eagle is a documented predator of domestic sheep (Warren et al. 2001). Absence of ungulates in the diet of golden eagles was also found by Skouen (2012) despite the fact that both my nest and her nest were located in areas where sheep and lambs were released to graze in the spring and summer. In the study of Skouen (2012) wild reindeer herds were also in proximity of the nest. However, carrion is usually consumed in situ and not necessarily brought to the nest (Sánchez-Zapata et al. 2010).

The real impact of the golden eagle on livestock is debated. There is seemingly no relationship between the density of breeding golden eagles in an area and the amount of attacks on sheep, on the contrary there is more golden eagle attacks on sheep in areas with small populations of eagles, but also in years of low breeding success (Gjershaug & Nygård 2003; Loland 2014). Loland (2014) related this to the availability of the non-domestic prey. When the preferred prey is scarce, it seems the eagle turn to sheep as an alternative. My study and that of Skouen (2012) only covered the diet in May-June, and the diet probably changes considerably between seasons. Watson (2010) found that ungulates were utilized most during winter as golden eagles frequently scavenged carrion.

Scavenging carrion is a very common behaviour in golden eagles, and is therefore often seen around newly deceased livestock (Sánchez-Zapata et al. 2010). However, whether or not the golden eagle was the primary cause of death or if other factors are involved is often difficult to decide (Watson 2010).

As expected the breeding rough-legged buzzards showed a much less diverse diet than the golden eagle. Of the 253 prey the most important prey were *Microtus* voles, which made up 71% of the delivered prey at the nest, and 69 % of the total body mass. Thrushes made up 15 % of the total body mass delivered at the nest, and other microtine rodents than *Microtus* voles were also utilized. This is in accordance with other studies assessing the diet of rough-legged buzzards (Sylvén 1978; Hagen 1989) The large proportion of *Microtus* voles found in the diet of the rough-legged buzzard in my study suggests that the rough-legged buzzard responded functionally to *Microtus* voles.

Despite the high abundance of Norway lemming in my study area, the rough-legged buzzard did not respond functionally to Norwegian lemmings as has been found in other studies. Hellström et al. (2014) found 41 % of the prey items of rough-legged buzzards to be Norwegian lemming, and that the buzzards had a type II functional response to the lemmings. Their study was conducted in sub-arctic regions of northern Sweden. The very small proportion of lemmings in my study may reflect the different habitat use of Norwegian lemmings and *Microtus* voles. In my study the rough-legged buzzard nest was located near a clear-cut area, and such habitat is highly associated with *Microtus* voles (Sonerud 1986).

With such a dominance of *Microtus* voles in the diet, the breeding pair of rough-legged buzzard in my study can be considered as food specialists (Andersson & Erlinge 1977). The cyclic fluctuations in densities of small mammals such as *Microtus* voles are known to show a strong relationship with the reproductive performance of their predator especially in specialist predators. However, in arctic Russia, Pokrovsky et al. (2014) found that the breeding success of the rough-legged buzzard did not decrease with low rodent numbers. It seemed that the cumulative abundance of the available alternative prey was more important for the breeding success of the rough-legged buzzards. There was a one-year lag from when the peak in the cumulative abundance of prey to the peak in reproduction of the rough-legged buzzard. The rough-legged buzzard was therefore regarded by Pokrovsky et al. (2014) as a food generalist.

A long-term study using video monitoring to analyse the diet of the rough-legged buzzard in the boreal zone under all phases of the rodent cycle could reveal how low availability of preferred prey affects the level of prey specialisation and the breeding success in rough-legged buzzards.

In both nests that I studied, the parental roles was as expected from the literature (Collopy 1984). The male was the main provider of food, as the male rough-legged buzzard delivered 75 % of the prey, while the male golden eagle made 57 % of the deliveries. The female brood and feed the young. The probability that a prey was delivered by the male was highest before midday for both study species. These results may reflect the activity of their prey being highest in the morning hours. Male raptors typically only visit the nest to deliver a prey, and a lot of time is spent perching some distance from the nest (Collopy & Edwards Jr 1989).

The male golden eagle was more likely than the female to deliver birds. This was also found by Skouen (2012). The fact that the male golden eagle delivered more birds can be related to his smaller size. Most raptors exhibit reversed sexual size dimorphism; where the male is smaller than the female (Newton 2010). The hypothesis explaining how and why this evolved is debated (Slagsvold & Sonerud 2007; Sonerud et al. 2014b). However, as a result the smaller male is more agile than the female and can therefore hunt agile prey such as birds with higher success (Newton 2010).

At the golden eagle nest the female delivered 43 % of the prey items. The probability that she delivered a microtine rodent rather than another prey was higher than for the male. The female spend more time on and near the nest than the male (Collopy 1984). The female's high probability of delivering a microtine rodent may therefore be a result of the high density of microtine rodents increasing the probability of detecting one around the nest. Once detected these prey may be easily captured. Furthermore, microtine rodents were also more likely than other prey, and than other mammals to be taken under high ambient temperature. This was also the case for lemmings relative to other prey. Their high metabolic rate forces lemmings and voles to forage at a regular basis, which would make them more active at higher ambient temperatures compared to other prey (Lehmann & Sommersberg 1980), which may be why they are taken during high ambient temperatures.



The analyses from the rough-legged buzzard nest showed that the probability that a bird was delivered at the nest rather than a mammal was lower during rainfall than at other times. This may indicate that birds are less available as prey relative to mammals during rainfall, because they are less active foraging. Birds are generally negatively affected by rainfall as manifested by lowered survival and reproductive success (Öberg et al. 2015).

With increasing age, the nestlings were more likely to feed unassisted. The predicted age of the nestlings when the nestlings would be as likely to feed unassisted as being fed by the female was at 47 days for the golden eagles, and 41 days for the rough-legged buzzard (where the nestlings fledged at around 40 days). However, the breeding period is a very energy demanding period, particularly for the female, prolonged feeding by the female can be the a way to control the allocation of food between her own need and that of the offspring (Brodin et al. 2003; Sonerud et al. 2013). At what time she terminates feeding the nestlings and starts assisting the male in providing prey depend on prey type (Sonerud et al. 2014a; Sonerud et al. 2014b) and may also depend on amount of food being available (Byholm et al. 2011). In theory if there is extra food the female can reduce her work effort and enhance her fitness and survival by feeding off the excess food the male brings to the nest (Sonerud et al. 2013). Experimental studies where supplement food is provided during the nesting period found that food supply had an effect on behaviour and fitness of both parents, but the effect was much stronger in females (Dawson & Bortolotti 2002; Eldegard & Sonerud 2010). The supplemented food reduced the work effort by both parents, most in females. The females contributed less to food providing, and their mass loss was lower than what was found in control females (Eldegard & Sonerud 2010). The excess food did not seem to have an effect on the offspring quality, which suggest that the additional food was beneficial for the parents and was used to reduce the high costs of reproduction (Dawson & Bortolotti 2002; Eldegard & Sonerud 2010). The golden eagle nestlings were fed about a week longer at the nest I studied than at the nest that Skouen 2012 studied, which fits with the fact that my study took place at an extremely high population density of microtine rodents. This was also in line with my findings that the rough-legged buzzard nestlings were fed by the female as often as they fed unassisted right up to fledging.

The female rough-legged buzzard was more likely to deliver prey items during low ambient temperature, and the nestlings were also more likely to feed unassisted at lower ambient

temperature, and as they became older. This could be due to the female's presence at the nest declining during cold weather, and as the nestling grew older. When it was warm the female was likely to be in the nest shielding the nestlings, however as the ambient temperature dropped she could be out hunting, hence more deliveries. Based on my observations from the recorded material I suggest that her absence created an opportunity for the nestlings to feed unassisted, which was virtually impossible while she was present, as she insisted on feeding the nestlings, even though they obviously were able to feed unassisted.

In both nests there was an effect of nestling age and prey size on the probability that the nestlings would feed unassisted. The buzzard nestlings were also more likely to feed unassisted when a mammal was delivered. Raptor nestlings are dependent on the female to prepare prey items to a suitable size that they are able to ingest (Newton 2010; Sonerud et al. 2014a). According to the feeding constraint hypothesis the gape size limit and swallowing capacity increase with age of the nestlings (Steen et al. 2010), and they are therefore more able to feed unassisted with increasing age. The ingestion rate is higher for small prey than for large prey and avian prey, which require more preparation. The ingestion rate is also higher for raptors with mammalian prey as their main diet, like rough-legged buzzards, than for raptors that mainly prey on avian prey (Slagsvold & Sonerud 2007).

At the golden eagle nest grouse (*Tetraonidae* sp.) were more likely to be delivered earlier in the season than other birds, and thrushes (*Turdus* sp.) were more likely to be delivered at the nest later in the season than other birds. Skouen (2012) also found that deliveries of grouse decreased throughout the season. Though this has not been investigated it could be linked to the fact that delivering smaller prey (such as thrushes) to the nest as nestlings grow older may benefit the parents because they are then relieved from preparing the prey as the nestlings will be able to feed unassisted. However, the results may also reflect the shifting availability of thrushes and grouse throughout the season, which shows the same pattern. During the initial stages of breeding the grouse species such as willow grouse are much more prone to predation (Hannon et al. 2003). Thrushes hatch later in the season so fledglings of thrushes then become available towards the end of the season.

Video monitoring is a non-invasive, cost-efficient method that provides a fairly accurate description of the composition of the diet of a raptor (Lewis et al. 2004; Selås et al. 2007; Tornberg & Reif 2007). However, there are some limiting aspects associated with this method. It was challenging to identify the prey item to species level with confidence, and identification was therefore often settled at the genus level to be on the safe side. Sometimes a prey item was visible only for a few seconds. As the nestlings grew older and became more aggressive they would shield the prey from the parents or siblings or ingest it immediately. Direct sunlight on the nest and the camera lens also created a visual challenge. These factors made some prey identification difficult. An additional camera to view the prey from another angle would have been helpful.

To conclude my results are largely in accordance with earlier studies made on the diet of the golden eagle and the rough-legged buzzard, but suggests in addition that voles and especially Norwegian lemmings in a peak vole year may be a more important food source than earlier assumed for the golden eagle. There were no recorded deliveries of wild reindeer or domestic sheep at the golden eagle nest, or at the other video monitored nest in Norway. The rough-legged buzzards responded functionally to *Microtus* voles, as expected from previous literature. The female of both species stayed in the nest feeding the nestlings longer than necessary in regard to what time the nestlings were able to self-feed. This may be due to the fact that prey was abundant and that the prolonged stay was a strategy to enhance the females own fitness and thereby future survival. The probability that the nestlings would feed unassisted increased with their age, and with decreasing size of the prey item that was delivered at the nest. The rough-legged buzzard nestlings was also more likely to feed unassisted at low ambient temperature, and when the prey delivered was a mammal rather than a bird. This may be associated with the fact that ingestion rate is higher for small prey than for large prey and avian prey, which require more preparation. The extent to which the various prey are included in the diet of the golden eagle and the rough-legged buzzard seems to be a result of their varying availability in time and space. More research can be focused on long term studies using video monitoring over all phases of a Microtine rodent cycle to determine the real effect voles and lemmings have on the breeding success of the golden eagle and rough-legged buzzard, and to accurately understand their roles as predators in the ecosystem they occupy. To do this a thorough estimation of the prey abundance in the study area should be conducted.

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