

Prey selection and handling in the eagle owl (*Bubo bubo*) by video monitoring at nest

Byttedyrseleksjon og håndtering hos hubro (*Bubo bubo*) ved videoovervåking på reir

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## Abstract

Prey selection and handling of prey in a breeding pair of the eagle owl (*Bubo bubo*) were studied by video monitoring at a nest in southwestern Norway. The eagle owl's diet had a diverse composition of species. Of the 51 prey items recorded delivered at the nest, 47% were mammals, 39% were birds, and 8% were frogs. Mountain hare (*Lepus timidus*) was the most abundant prey type, and comprised 28% and 57% by number and mass, respectively. As much as 35% of the delivered prey items were birds related to wetland areas, and thus wetlands appeared to be important habitats for the eagle owls in my study area. The probability that a prey item delivered at the nest was a hare increased with increasing ambient temperature and with closeness in time to solar midnight, i. e. with increasing darkness. The corresponding probability for birds as prey decreased throughout the evening and beyond throughout the subsequent morning, while for small mammals as prey the probability increased throughout the evening and beyond throughout the subsequent morning, and with decreasing ambient temperature. The probability that a prey item delivered was a frog increased with decreasing ambient temperatures. A delivery of a hare was more likely followed by another delivery of a hare the longer time had elapsed since the previous delivery. For birds the pattern was opposite, a delivery of a bird was more likely followed by another delivery of a bird the shorter time had elapsed since the previous delivery. Birds were the only prey type in which decapitation, i.e. removing of the head, occurred prior to delivery at the nest, and the probability of a bird being decapitated increased with increasing darkness. The probability that the female eagle owl feed the nestling rather than the nestling fed unassisted decreased with nestling age and increased with body mass of prey. The probability that the nestling swallowed a prey item whole decreased with increasing body mass of prey. The handling time of a prey increased with increasing body mass of prey. The number of meals from a prey item increased with an increase in body mass of prey, and was higher if the prey item was a mammal than if it was a bird, and higher if the female fed the nestling rather than the nestling fed unassisted. When the nestling fed unassisted, the ingestion rate (g/min) decreased with increasing body mass of prey, mainly because the nestling was unable to swallow larger prey items whole. However, data from more nests, and from nests with more than one young, are needed to verify the trends found in my study.

## Sammenheng

Seleksjon og håndtering av byttedyr hos et hekkende par av hubro (*Bubo bubo*) ble undersøkt ved videoovervåking av et reir i Sørvest-Norge. Hubroens diett hadde en allsidig artssammensetning. Av de 51 byttedyrene som ble registrert levert på reiret, var 47% pattedyr, 39% fugl og 8% frosk. Hare (*Lepus timidus*) var den mest tallrike arten, både i antall (28%) og masse (57%). Så mye som 35% av antall arter levert på reiret var fugler som hadde tilknytning til våtmarksområder. Våtmarksområder viste seg dermed å være viktige habitat for hubroen i mitt studieområde. Sannsynligheten for at et byttedyr levert på reiret var en hare økte med økende temperatur, og økte med nærhet i tid til astronomisk midnatt, det vil si jo mørkere det var. Sannsynligheten for at et levert byttedyr var en fugl minsket utover kvelden og videre utover påfølgende morgen. Sannsynligheten for at et levert byttedyr var et småpattedyr økte utover kvelden og videre utover påfølgende morgen og økte ved lavere temperaturer. Sannsynligheten for at et levert byttedyr var en frosk økte med lavere temperatur. Levering av en hare ble med større sannsynlighet etterfulgt av levering av nok en hare jo lengre tid siden forrige levering. For fugl gjaldt det motsatte; levering av en fugl ble med større sannsynlighet etterfulgt av levering av nok en fugl jo kortere tid siden forrige levering. Fugler var den eneste byttedyrtypen som hubroen dekapiterte (fjernet hodet) før levering på reiret. Sannsynligheten for at en fugl var dekapitert før den ble levert til reiret økte jo mørkere det var. Sannsynligheten for at hunnen foret ungen heller enn at ungen spiste selv minket med økende alder på ungen og økte med økende vekt på byttedyret. Det var mindre sannsynlighet for at ungen svelget byttet helt med økende vekt på byttedyret. Håndteringstiden til et byttedyr økte med økende byttedyrvekt. Antall måltider for hvert av byttedyrene økte med økende byttedyrvekt, og var høyere hvis byttedyret var et pattedyr enn hvis det var en fugl, og høyere hvis hunnen foret ungen heller enn ungen spiste selv. Inntaksraten (g/min) når ungen spiste selv minket for byttedyr med økende kroppsvekt, hovedsakelig grunnet ungens manglende mulighet til å svelge større byttedyr hele. Data fra flere reir, og fra reir som inneholder mer enn én unge, trengs for å kunne beskrive trendene som er funnet i dette studiet med større sikkerhet.



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## Introduction

The swallowing capacity is considered as a limitation for birds that swallow their prey items whole, as it constraints their choice of prey (Slagsvold & Sonerud 2007). Raptors capture prey items with their feet, and have developed their bills as a tool for preparing larger prey into edible parts (Slagsvold & Sonerud 2007). This enables the raptors to capture and consume relatively large prey for their size (Steen et al. 2010). However, they can only tear apart small portions at a time, hence longer time is needed to prepare the prey (Slagsvold and Sonerud 2007; Steen et al. 2010). Provisioning of prey, including preparing prey for dependent offspring, is thus a trade-off between benefits for the nestlings that prevent the swallowing threshold to be a constraint, and the cost for the parents in lost time for self-foraging (Ponz et al 1999; Steen et al. 2010). The larger bones and thicker skin and skull make larger prey items less profitable as food, because less of the prey item is consumed and more time spent on preparation of the prey item (Slagsvold & Sonerud 2007; Slagsvold et al. 2010). The ingestion rate is calculated as prey mass consumed per unit handling time, and is a measure of handling efficiency. The ingestion rate has been found to decrease with prey size (Sullivan 1988; Slagsvold & Sonerud 2007). Thus, as the main food provider during the breeding season, the male should be smaller than the female to be able to catch smaller and more profitable prey for the nestlings. This is termed the ingestion rate hypothesis (Slagsvold & Sonerud 2007). The pattern of reversed sexual size dimorphism (RSD) in raptors, where the male is smaller than the female, is suggested to support this hypothesis (Slagsvold & Sonerud 2007).

Raptors with a wide diet are particularly suitable for a study of prey handling because of their potentially large variation in handling modes and handling time. One such generalist raptor is the eagle owl (*Bubo bubo*). The eagle owl occurs in the western Palearctic and is the largest owl in Europe (Cramp 1985; Oddane & Undheim 2007), with an average wingspan of c. 160 cm in males and c. 170 cm in females, and a body mass in the autumn and winter on average c. 2400 g and 3000 g, respectively (Hagen 1952). The eagle owl is primarily a nocturnal bird, and prefers habitats shielded from human residence with good hunting grounds and nesting opportunities in temperate, boreal, steppe and Mediterranean regions (Cramp 1985). The male hunts and delivers the food to the female and the nestlings while the female incubates, feeds and broods

the nestlings (Cramp 1985). The male capture one prey at a time and delivers it to the female at or near the nest (Cramp 1985). This makes the eagle owl a single prey loading central place forager (Sonerud 1985). When the nestlings are about one month old the female does not longer need to brood them, and therefore starts to participate in hunting for the offspring (Hagen 1952; Cramp 1985).

The diet of the eagle owl is fairly well studied by observations, collection of prey remains and by analyzing pellets (Curry-Lindahl 1950; Hagen 1952; Willgoths 1974; Mysterud & Dunker 1982; Melis et al. 2011). The composition of the diet might differ from year to year due to corresponding differences in the availability of prey. The variation in diet between countries and among biomes can be quite large, as the variety of prey availability is large (Willgoths 1974). Willgoths (1974) studied the diet of the eagle owl in Norway by analyzing pellets, stomach contents and prey remains, where much of the material was based on earlier findings. He found that birds accounted for 64% of all vertebrates and were the major group of prey in the eagle owl's diet, with seabirds in the families Laridae, Anatidae and Alcidae as the most important ones. Mammals represented 33% of the vertebrates in total, with small rodents as the major group with dominance of brown rat (*Rattus norvegicus*) and field vole (*Microtus agrestis*). Amphibians, fishes and invertebrates were minor groups of prey (Willgoths 1974).

The aim of my study was to investigate prey selection and handling of different prey types and prey sizes in a breeding pair of eagle owls by video monitoring at their nest. Video monitoring has been used in several previous studies as a method to obtain a better knowledge and more accurate estimates of the diet of several species of raptors (Rønning 2007; Homme 2008; Steen et al. 2010; Steen et al. 2011a; Steen et al. 2011b; Skouen 2012). I wanted to analyze the composition of the recorded prey items delivered at the nest, and what affected the eagle owl's selection of different prey groups. Further, I wanted to investigate whether some prey items were more prepared, in terms of decapitation, than others when they were delivered at the nest, and what affected preparation of prey items prior to delivery. I also wanted to look at the different components of prey handling in the nest. I wanted to investigate what affected whether or not the female fed the nestling, which factors influenced whether or not the nestling swallowed a prey item whole, and which factors that had an impact

on the handling time of a prey item, the number of meals and the ingestion rate. To my knowledge, video recording as a method to investigate the diet composition of the eagle owl has never been done before. Video recordings of prey deliveries at the nest of a breeding pair of eagle owls will provide a more accurate measure of the real quantity of food delivered at the nest and improve the knowledge about the handling of prey by the eagle owl.

## Methods

### Study area

The study was conducted from late May to late June 2012 in Hå municipality in Rogaland county, in southwestern Norway (58°49'N; 5°43'E). This is a mountainous region with hills and valleys. Grass- and coastal heathland is dominating the vegetation due to several thousand years of grazing and heath burning, as well as the nutrient poor bedrock (Puschmann 2005). This favors heathland species and heather (*Calluna vulgaris*), but juniper (*Juniperus communis*) and some birches (*Betula pubescens*) are also present in the landscape. These areas are widely used as grazing areas for sheep (*Ovis aries*), and fertilization of the soil is occurring in some parts of the study area, creating grasslands. There are small lakes between the uncovered hills, and the coastline of the region faces the North Sea. One smaller part of the study area is an area of lowland fields, which is relatively flat and used as farmland (Puschmann 2005).

### Video monitoring

I video monitored an eagle owl nest for 39 days, starting 22 May. The brood consisted of one nestling, and the nest was situated on a small mountain ledge. By comparing my video shots with the photos in Penteriani et al. (2005), the nestling was estimated to being hatched 1 May, hence it was 22 days old when the video monitoring started.

Prey deliveries and handling times were recorded using two CCD (charged-coupled device) cameras with motion sensors, installed at the nest. A new video file started when movements in the nest triggered the motion sensors in the cameras, with the extent of the movement deciding if the sensors would react. The sensitivity of the motion sensors was set to 5% at first, but was reduced to 1% and 0%, respectively, as much of the handling was missing when the sensitivity was at 5% due to more movements needed for the sensors to react. The cameras were not installed until late May to minimize risk of the parents deserting after visits by humans to the nest. One of the cameras was located c. 2 m above the nest to get an overview, while the second camera was placed within the nest shelf to get detailed information about the prey

deliveries. The cameras were equipped with infrared lights (IR-lights), which made it possible to record activity at night. Each camera was connected to a mini digital video recorder (mini DVR), located in a waterproof plastic container. The exact date and time was set at the mini DVR to get as accurate measures of deliveries and handling times as possible. The recordings were stored on SD-cards and transferred to a laptop successively. Each SD-card stored 32 GB of data, but for unknown reasons the cards did not store more data than 20 GB, and needed to be replaced with an empty SD-card every second or third day. Power was obtained from two sealed 12 V lead batteries. To prevent disturbance when changing SD-cards and batteries, the recording device was placed 100 m away from the nest by use of a video cable. This setup is a modification of the method described by Steen (2009).

Data on precipitation, temperature and wind during the period of video monitoring were obtained from Obrestad fyr weather station, which was the nearest weather station, located in Hå Municipality in Rogaland County (58°39,55'N; 5°33,32'E). All three weather parameters were logged once every hour.

## **Analyzing delivered prey**

Nearly 344 000 video files from the nest were stored and later studied in detail. Most of the files did not contain prey deliveries or prey handling. Therefore, c. 7000 files, including prey deliveries and handling, were further analyzed. The prey items recorded on video were studied in detail by using a projector, and identified to the lowest taxonomic level possible, most of them to species or family. By using a time indicator located at the bottom left corner of the picture, I logged date and time of delivery of prey as time of arrival by the delivering parent. The sex of the delivering parent was determined, as well as whether the prey item was delivered decapitated, i.e. with head removed. Each prey item delivered at the nest was scored to one of four main categories: hare, other mammal than hare, bird or frog, which were used in the statistical analysis later on. Subsequently, I examined whether a prey item delivered at the nest belonged to the same prey category as the previous prey item delivered, to find out if the eagle owl focused on the same prey category on successive hunts for prey.

Body mass of avian prey items was obtained from the literature (Cramp and Simmons 1983; Cramp 1985; Cramp 1988; Cramp & Perrins 1994), because the intraspecific variation in body mass of adult birds is relatively small (Steen 2004; Steen et al. 2010). I subtracted 12.9% of the gross body mass for birds delivered decapitated (Slagsvold & Sonerud, unpublished). The 14 hares delivered at the nest were compared with each other to obtain a relative body mass, which made it easier to estimate a reasonable body mass for each individual hare. By comparing prey items of the same species with each other in order to regulate for intraspecific differences in mass, the estimations of body mass of small mammals were set. The body mass of a frog taken as prey was set to 20 g based on estimates from trapped specimen (Steen et al. 2011b). For 3 of the 51 prey items delivered at the nest the prey mass could not be obtained due to missing data after delivery or because the prey was difficult to view, or brought out of vision of the camera lens.

I estimated handling time for each prey item delivered to the nearest second. During each feeding session I recorded whether the female assisted the nestling in feeding or if the nestling fed unassisted. When the female assisted the nestling in feeding, handling time was defined as the time elapsed from the female bent her head down for the first time to prepare the prey item until the prey item had been completely consumed by the nestling and the nestling's swallowing movements ended (Steen 2010). Handling time when the nestling fed unassisted was defined as the time elapsed from the first time the nestling bent its head down until the item had been consumed and the swallowing movements ended. When a prey item was swallowed whole, the handling time was taken as the time elapsed from when the nestling received the prey item from its parent, or from when the nestling bent its head down to get hold of the prey, until the last swallowing movement ended (Steen 2010). I excluded plucking of prey as a part of the handling time due to missing or incomplete recordings of this activity. Plucking of prey appears to be of little importance when the eagle owl is handling its prey (Willgohs 1974; Mysterud & Dunker 1982). Cleaning of the nest was not included in the handling time because it seemed to be an activity that occurred randomly. Pauses longer than 5 s were excluded from the handling time, and were summed up and subtracted from gross handling time, to obtain a net handling time without the pauses included. If a pause in handling of prey

was longer than one hour, the corresponding feeding sessions were recorded as two separate meals. For 17 of the 51 prey items delivered at the nest, handling time was not obtained due to technical failure of the equipment or due to the behavior of the nestling. When the loss in handling time was caused by the nestling itself, it was either because the nestling hid under a juniper bush in the nest, or because the nestling was out of sight of the camera or had its back turned against it.

## **Statistical analysis**

The statistical analysis and the related figures were made by use of the statistical software JMP ® version 10.0.0. The figures in the result section are only intended as illustrations of the main findings, because a figure made in JMP only takes into account the explanatory variable illustrated independently of the other explanatory variables in a multivariate model. Thus the p-values of the figures are different from, and based on other quantities of numbers, than the p-values related to the explanatory variables from multivariate models in the tables.

To test the effects of multiple explanatory variables and their interactions on a dependent binomial response variable, logistic regression by the likelihood ratio test was used. Backward elimination was used to remove non-significant variables from the model, one at a time, until the model included only explanatory variables that were significant at the 5% level.

The response variables tested were whether the delivered prey item was a hare or not, whether the delivered prey item was a bird or not, whether the delivered prey item was a mammal other than a hare or not, and whether the delivered prey item was a frog or not. Further, I tested whether or not the delivered prey item was of the same prey type as previous item delivered, and whether or not the prey item delivered was decapitated prior to delivery, whether the female fed the nestling or the nestling fed unassisted, and whether the nestling swallowed the prey item in one piece or not.

The explanatory variables used to test which factors affected whether the delivered prey item was a hare, whether the delivered prey item was a bird, whether the delivered prey item was a mammal other than hare and whether the delivered prey item was a frog, were the age of the nestling, the deviation from solar midnight, if the delivery was before or after solar midnight, and the weather parameters as wind speed, ambient temperature (°C) and precipitation, the latter being total precipitation (mm) the last hour before delivery. The interaction between the deviation from solar midnight and whether the prey was delivered before or after solar midnight was also included. Solar midnight was defined as the time when the sun was at its lowest position under the horizon. This was set as an average for the study period, which was at 01.37 hours.

The explanatory variables used to test whether the delivered prey item was of the same prey type as the previous item delivered, were deviation from solar midnight, if the delivery was before or after solar midnight, time since the previous delivery, prey type, and the interaction between the deviation from solar midnight and whether the prey was delivered before or after solar midnight, and the interaction between time since the previous delivery and prey type. When calculating time since the previous delivery I excluded breaks in the recordings that lasted for more than 27 hours, because most likely there would have been at least one missed delivery of prey when the break was more than 27 hours. Frog was excluded as prey type in this model due to unstable estimates caused by small sample size.

The explanatory variables used to test which factors affected whether the prey item was delivered decapitated, were the age of the nestling, whether the female fed the nestling, prey type, gross body mass of prey (g), deviation from solar midnight, whether the prey item was delivered before or after solar midnight, the interaction between gross body mass (g) and prey type, and the interaction between deviation from solar midnight and whether the prey item was delivered before or after solar midnight.

The explanatory variables used to test whether the female fed the nestling or the nestling fed unassisted, were the age of the nestling, gross body mass of prey (g), prey



type, the interaction between prey type and gross body mass of prey (g), and the interaction between age of the nestling and gross body mass of prey (g).

The explanatory variables used to test whether the nestling swallowed the prey whole or not, were the age of the nestling, the net body mass of the prey items, and the interaction between those two.

I used a generalized linear model (GLM) with Poisson distribution to test which explanatory variables that might have had an effect on the number of meals per prey item. The explanatory variables tested were the age of the nestling, prey type, net body mass of prey (g), whether the female fed the nestling, the interaction between net body mass of prey (g) and the age of the nestling, the interaction between net body mass of prey (g) and whether the female fed the nestling, and the interaction between prey type and net body mass of prey (g).

Handling time and ingestion rate were continuous response variables, and thus linear regression was used to test which variables affected them. The data in the linear regression analysis were  $\log_{10}$  transformed to obtain normal distribution of the residuals. The explanatory variables that might have had an effect on handling time were the age of the nestling, net body mass of prey (g), prey type, and the interaction between net body mass of prey (g) and prey type. The explanatory variables that might have had an effect on the ingestion rate of the nestling, were the age of the nestling, gross body mass of the nestling (g), whether the female fed the nestling, prey type, and the interaction between gross body mass of prey (g) and prey type.

## Results

### Prey delivered at the nest

A total of 51 prey items were recorded delivered at the eagle owl nest during the period of video monitoring, of which three prey items were not possible to identify to any taxonomic level (Table 1). In total 47.2% of all prey items delivered at the nest were mammals, 39.3% were birds, and 7.8% were frogs. The unidentified prey items accounted for 5.9% of prey delivered at the nest (Table 1). Mountain hare (*Lepus timidus*) was the most common prey, and accounted for 27.5% of total prey by number and 57.2% of total estimated body mass (Table 1). Northern lapwing (*Vanellus vanellus*) was the most common bird by number and comprised 7.8% of all prey items delivered, followed by the common snipe (*Gallinago gallinago*) and the Eurasian woodcock (*Scolopax rusticola*), which comprised 5.9% each. Common raven (*Corvus corax*) accounted for only 2.0% of total prey by number, but comprised 9.5% of the total estimated body mass, making it the most important species of bird by total estimated body mass of prey delivered at the nest (Table 1). Wood mouse (*Apodemus sylvaticus*) and other small rodents accounted for 5.9% and 9.8% of total prey by number, respectively, but only contributed with 0.7% and 1.2% of total estimated body mass of prey delivered at the nest, respectively (Table 1).

The prey items were assigned to four main categories (Table 2). By distributing the unidentified prey items among these four main categories, other mammals than hare comprised 20.8% of total prey number delivered at the nest (Table 2).

Table 1. Prey items delivered at an eagle owl nest, assigned to prey categories by number (N) and percentage (%). Share of estimated body mass of prey is given both for the average individual in a category and for the category as a whole, by mass (g) and percentage (%).

Prey category	Prey number (N)	Prey number (%)	Proportion of number of known prey (%)	Unit body mass (g)	Total estimated body mass (g)	Proportion of total body mass (%)
Eurasian woodcock ( <i>Scolopax rusticola</i> )	3	5.9	6.3	300.0	900.0	7.1
Hooded crow ( <i>Corvus cornix</i> )	2	3.9	4.2	500.0	1000.0	7.9
Duckling	2	3.9	4.2	125.0	250.0	2.0
Northern lapwing ( <i>Vanellus vanellus</i> )	4	7.8	8.3	200.0	800.0	6.3
Common snipe ( <i>Gallinago gallinago</i> )	3	5.9	6.3	100.0	300.0	2.4
Common raven ( <i>Corvus corax</i> )	1	2.0	2.1	1200.0	1200.0	9.5
Thrush sp. (Turdidae)	2	3.9	4.2	100.0	200.0	1.6
Common cuckoo ( <i>Cuculus canorus</i> )	1	2.0	2.1	100.0	100.0	0.8
Shorebird (Scolopacidae)	1	2.0	2.1	100.0	100.0	0.8
Bird unidentified	1	2.0	2.1	100.0	100.0	0.8
Birds (total)	20	39.3	41.9	2825.0	4950.0	39.2
Mountain hare ( <i>Lepus timidus</i> )	14	27.5	29.2	517.9 <sup>1</sup>	7250.6	57.2
Wood mouse ( <i>Apodemus sylvaticus</i> )	3	5.9	6.3	28.3 <sup>2</sup>	84.9	0.7
Water vole ( <i>Arvicola amphibius</i> )	1	2.0	2.1	150.0	150.0	1.2
Rodents	5	9.8	10.4	31.0 <sup>3</sup>	155.0	1.2
Mammal <sup>4</sup>	1	2.0	2.1	10.0	10.0	0.1
Mammals (total)	24	47.2	50.1	737.2	7650.5	60.4
Common frog ( <i>Rana temporaria</i> )	4	7.8	8.3	20.0	80.0	0.6
Unidentified	3	5.9				
Total	51	100.2	100.3	3582.2	12680.5	100.2

<sup>1</sup> Mean estimate (variation 150-1000 g)

<sup>2</sup> Mean estimate (variation 25-30 g)

<sup>3</sup> Mean estimate (variation 15-50 g)

<sup>4</sup> Most likely a shrew (Soricidae)

Table 2. Main categories of prey delivered at an eagle owl nest by number. The unidentified prey items are distributed among the four categories according to the proportion of these four categories among identified prey items.

Prey category	Prey number (N)	Prey number (%)
Hare	14.87	29.2
Other mammal	10.62	20.8
Bird	21.25	41.7
Frog	4.25	8.3
Total	50.99	100

## Hunting activity

Irrespective of whether the prey items were delivered at the nest in the evening or in the morning, i.e. before or after solar midnight, all were delivered within a time span of 9 hours from solar midnight, and most within 4 hours (Figure 1). The mean deviation from solar midnight for the prey deliveries was 2 h 1 min and 5 s  $\pm$  12 min and 47 s ( $2.018 \pm 0.213$  hours), while the median deviation was 1 h 42 min and 11 s (1.703 hours).

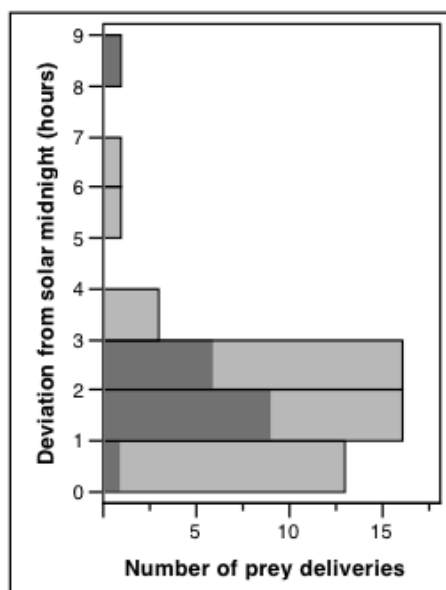


Figure 1. Temporal distribution of prey deliveries at the eagle owl nest, expressed as deviation from solar midnight (hours). The light areas of the columns are deliveries before solar midnight and the dark areas of the column are deliveries after solar midnight.

## Prey selection

### Selection of hare as a prey

The probability that a prey item delivered at the eagle owl nest was a hare rather than any other prey was significantly affected by deviation from solar midnight and by ambient temperature (Table 3).

Table 3. Logistic regression model of significant effects on the probability that a prey item delivered at the eagle owl nest was a hare. Whole model  $N = 48$ ,  $\chi^2 = 10.86$ ,  $df = 2$ ,  $p = 0.0044$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	- 3.167	1.516			
Deviation from solar midnight	- 0.764	0.365	1	6.58	0.010
Ambient temperature (°C)	0.346	0.144	1	6.65	0.0099

The probability that the prey item was a hare increased the closer to solar midnight it was delivered, irrespective of whether the delivery was before or after midnight (Figure 2). Thus, the darker it was, the more likely that the prey item delivered at the nest was a hare.

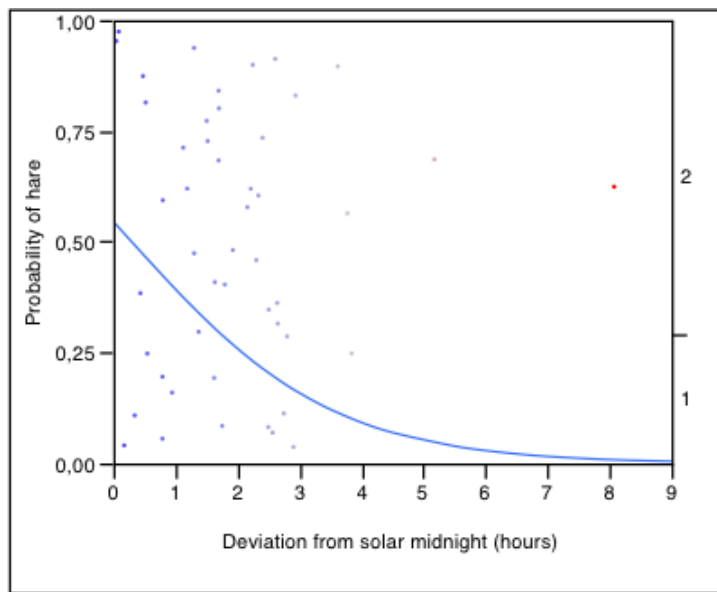


Figure 2. The probability that a prey item delivered at the eagle owl nest was a hare as a function of deviation from solar midnight (1 = hare, 2 = not hare). Whole model  $N = 48$ ,  $\chi^2 = 4.21$ ,  $df = 1$ ,  $p = 0.040$ .

The probability that the prey item delivered at the nest was a hare increased with increasing ambient temperature (Figure 3).

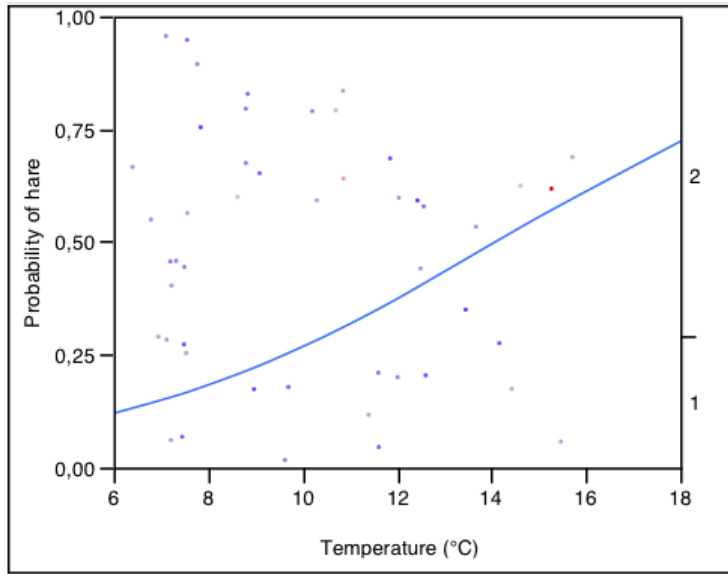


Figure 3. The probability that a prey item delivered at the eagle owl nest was a hare as a function of ambient temperature ( $^{\circ}\text{C}$ ) (1 = hare, 2 = not hare). Whole model  $N = 48$ ,  $\chi^2 = 4.28$ ,  $df = 1$ ,  $p = 0.039$ .

### Selection of bird as prey

The probability that the prey item delivered at the nest was a bird was significantly affected by the interaction between deviation from solar midnight and whether the delivery occurred before or after solar midnight, i.e. the effect of deviation from solar midnight differed between the evening and the morning (Table 4).

Table 4. Logistic regression model of significant effects on the probability that a prey item delivered at the eagle owl nest was a bird, with deviation after solar midnight as intercept. Whole model  $N = 47$ ,  $\chi^2 = 7.67$ ,  $df = 3$ ,  $p = 0.053$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-0.142	0.711			
Before/after solar midnight	-0.565	0.341	1	2.84	0.092
Deviation from solar midnight	0.029	0.320	1	0.01	0.93
Deviation from solar midnight *					
Before/after solar midnight	0.536	0.320	1	4.67	0.031

The probability that the prey item delivered at the nest was a bird decreased throughout the evening towards solar midnight (Figure 4a). After solar midnight, the probability that the prey item delivered at the nest was a bird decreased further throughout the morning (Figure 4b). Overall, the probability that a prey item delivered was a bird was higher in the morning than in the evening (Figures 4a, b).

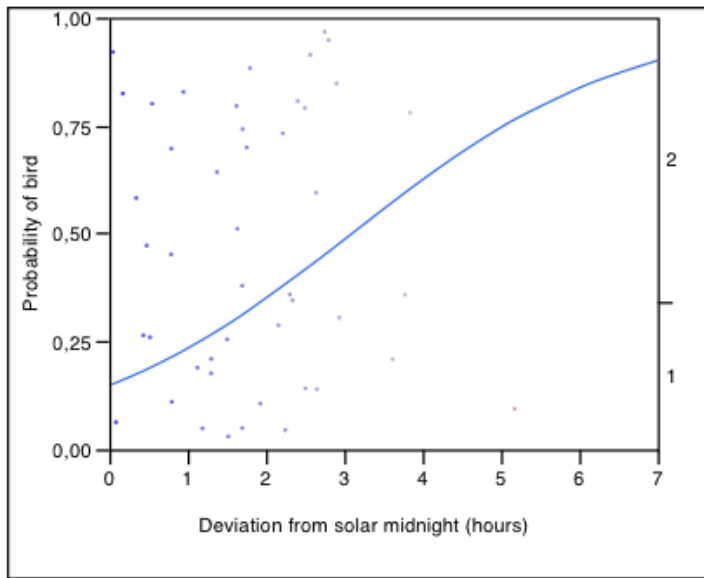


Figure 4a. The probability that a prey item delivered at the eagle owl nest was a bird as a function of deviation from solar midnight in the evening (1 = bird, 2 = not bird). Whole model  $N = 32$ ,  $\chi^2 = 3.34$ ,  $df = 1$ ,  $p = 0.068$ .

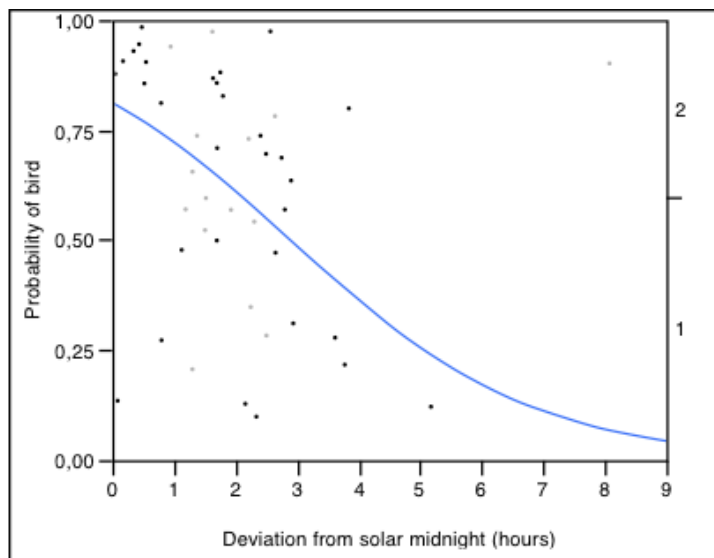


Figure 4b. The probability that a prey item delivered at the eagle owl nest was a bird as a function of deviation from solar midnight in the morning (1 = bird, 2 = not bird). Whole model  $N = 15$ ,  $\chi^2 = 1.59$ ,  $df = 1$ ,  $p = 0.21$ .

## Selection of other mammals than hare as prey

The probability that the prey item delivered at the nest was a mammal other than a hare was significantly affected by ambient temperature and by the interaction between deviation from solar midnight and whether the delivery was before or after solar midnight, i.e. the effect of deviation from solar midnight differed between the evening and the morning (Table 5).

Table 5. Logistic regression model of significant effects on the probability that a prey item delivered at the eagle owl nest was a mammal other than a hare. Whole model  $N = 47$ ,  $\chi^2 = 15.49$ ,  $df = 4$ ,  $p = 0.0038$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	-1.224	4.742			
Before/ after solar midnight	0.704	0.883	1	0.93	0.34
Deviation from solar midnight	1.864	1.784	1	3.00	0.084
Deviation from solar midnight *					
Before/after solar midnight	-2.365	1.780	1	10.25	0.0014
Temperature (°C)	-0.511	0.262	1	6.19	0.013

The probability that a prey item delivered at the nest was a mammal other than a hare decreased with increasing ambient temperature (Figure 5).

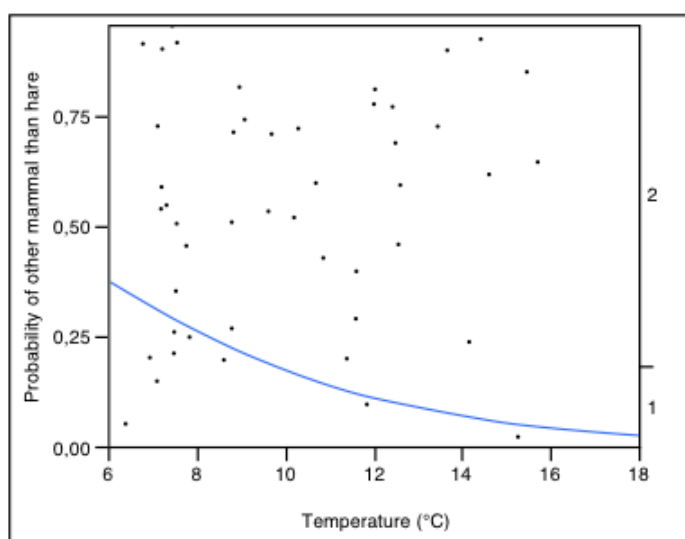


Figure 5. The probability that a prey item delivered at the eagle owl nest was a mammal other than a hare as a function of ambient temperature (°C) (1 = Other mammal than hare, 2 = Not other mammal than hare). Whole model  $N = 47$ ,  $\chi^2 = 2.97$ ,  $df = 1$ ,  $p = 0.085$ .



The probability that a prey item delivered at the nest was a mammal other than a hare increased throughout the evening towards solar midnight (Figure 6a), and increased from solar midnight throughout the morning (Figure 6b).

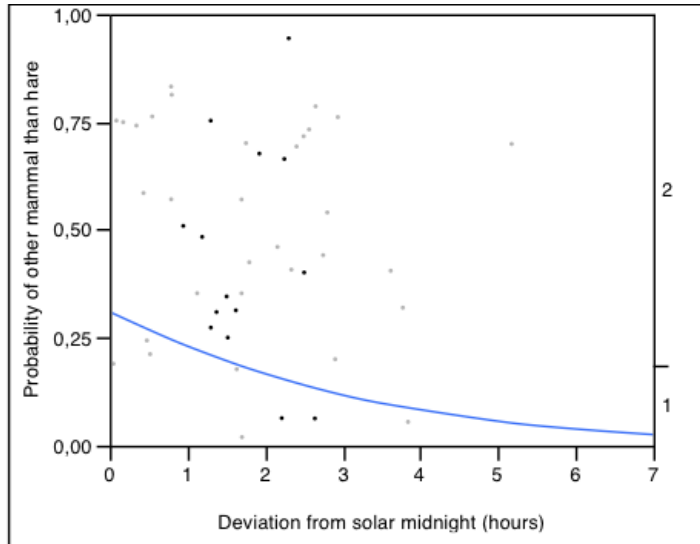


Figure 6a. The probability that a prey delivered at the nest was a mammal other than a hare as a function of deviation from solar midnight in the evening (1 = Other mammal than hare, 2 = not other mammal than hare). Whole model  $N = 32$ ,  $\chi^2 = 1.09$ ,  $df = 1$ ,  $p = 0.30$ .

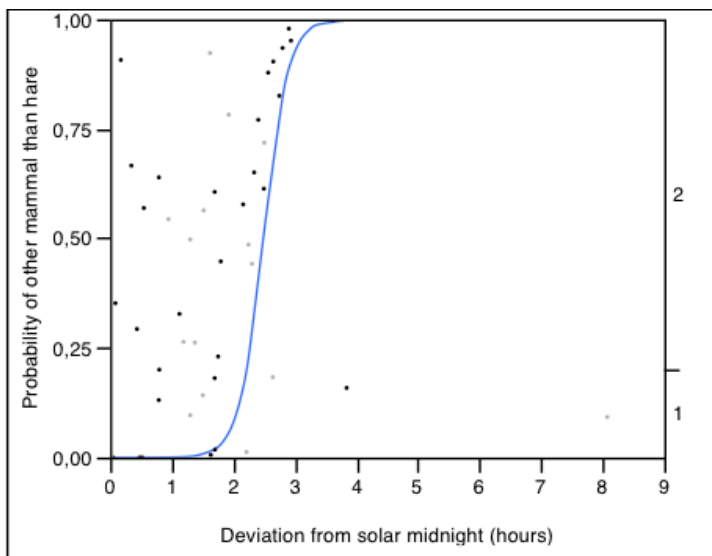


Figure 6b. The probability that a prey item delivered at the eagle owl nest was a mammal other than a hare as a function of deviation from solar midnight in the morning (1 = Other mammal than hare, 2 = not other mammal than hare). Whole model  $N = 15$ ,  $\chi^2 = 8.20$ ,  $df = 1$ ,  $p = 0.0042$ .

### Selection of frog as prey

The probability that a prey item delivered at the nest was a frog was significantly affected by whether the delivery occurred before or after solar midnight and by ambient temperature (Table 6). This result should be regarded with caution because the parameter estimates were unstable.

Table 6. Logistic regression model of significant effects on the probability that a prey item delivered at the eagle owl nest was a frog. Whole model  $N = 47$ ,  $\chi^2 = 10.49$ ,  $df = 2$ ,  $p = 0.0053$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	- 0.461	1676.333			
Before/after solar midnight	8.939	1676.318	1	4.91	0.027
Temperature (°C)	-1.244	0.978	1	7.24	0.0071

The probability that a prey item delivered was a frog decreased with increasing temperature (Figure 7).

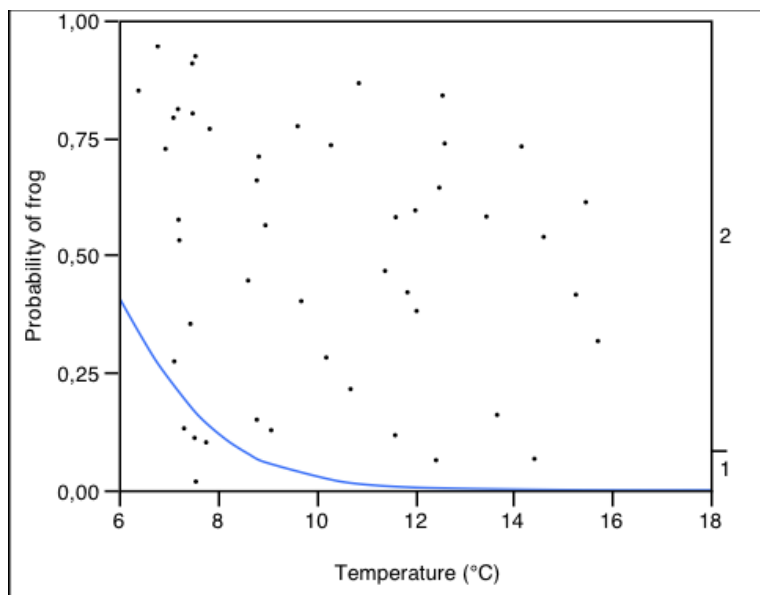


Figure 7. The probability that a prey item delivered at the eagle owl nest was a frog as a function of ambient temperature (°C) (1 = frog, 2 = not frog). Whole model  $N = 47$ ,  $\chi^2 = 5.58$ ,  $df = 1$ ,  $p = 0.018$ .

All prey items delivered at the nest that was a frog were delivered before solar midnight (Figure 8).

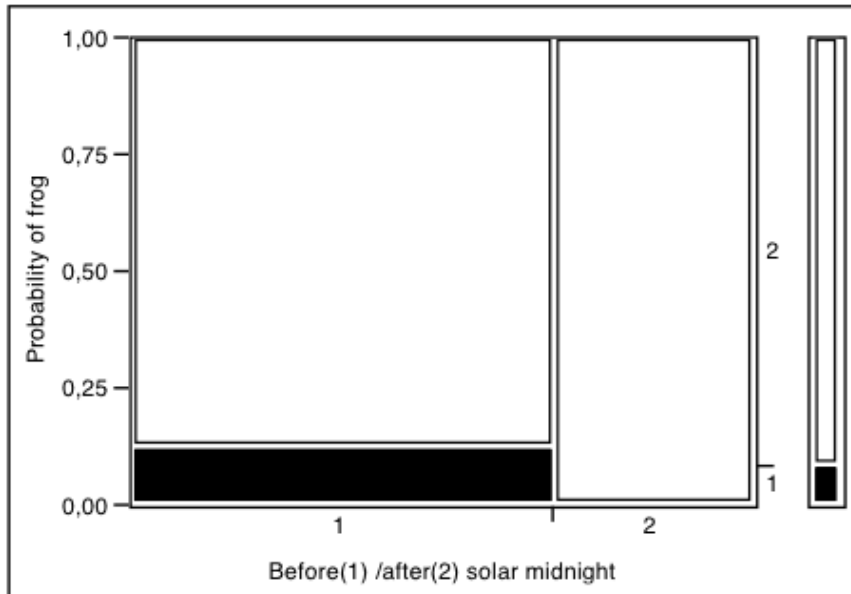


Figure 8. The probability that a prey item delivered at the eagle owl nest was a frog (shaded) as a function of whether the delivery occurred before or after solar midnight (1 = frog, 2 = not frog). Whole model  $N = 47$ ,  $\chi^2 = 3.25$ ,  $df = 1$ ,  $p = 0.072$ .

## Hunting strategy

The probability that a prey item delivered at the nest was of the same type as the previous item delivered was significantly affected by the interaction between prey type (bird, hare or other mammal than hare) and time since last delivery (Tables 7a,b). The effect of time since previous delivery on the probability that the item delivered at the nest was of the same type as the previous one was different for different prey types. Frog was not considered in this analysis because the parameter estimates were unstable, probably due to small sample size.

Table 7. Parameter estimates (a) and the following parameters from the likelihood ratio test, with the overall effect of prey type (b) from the logistic regression model of significant effects on the probability that the delivered prey item was of the same prey type as the previous item, with the prey type “other mammal than hare“ as intercept. Whole model N = 32,  $\chi^2 = 9.62$ , df = 5, p = 0.087.

a)

Explanatory variables	Estimate	SE
Intercept	- 0.357	0.636
Time since last delivery (h)	- 0.076	0.090
Prey type [1]	- 0.459	1.338
Prey type [2]	0.266	0.859
Time since previous delivery (h)*Prey type[1]	- 0.218	0.167
Time since previous delivery (h)*Prey type[2]	0.160	0.097

b)

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	- 0.357	0.636			
Time since last delivery (h)	- 0.076	0.090	1	1.23	0.27
Prey type			2	0.16	0.92
Prey type*Time since previous delivery (h)			2	8.17	0.017

The probability that a prey item delivered at the nest was a hare when the previous prey delivered at the nest was a hare increased with time since previous prey delivery (Figure 9).

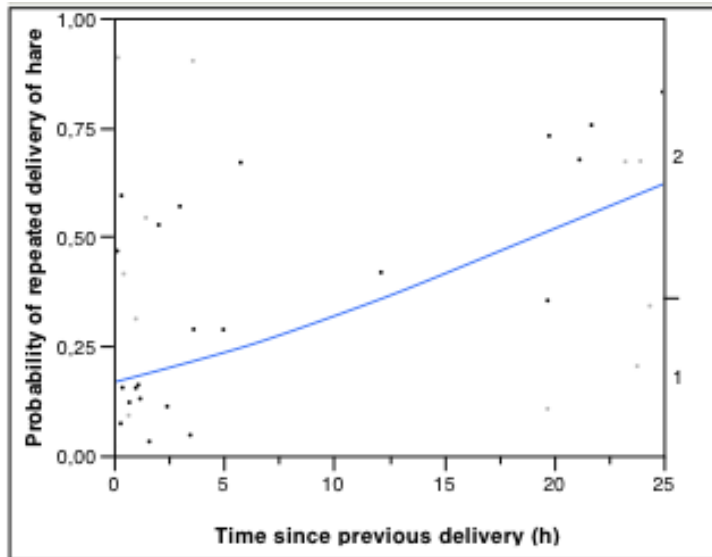


Figure 9. The probability that a prey item delivered at the eagle owl nest (N) was a hare when the previous prey item delivered (N-1) was a hare as a function of time since previous delivery, measured in hours (1 = hare, 2 = not hare). Whole model  $N = 11$ ,  $\chi^2 = 1.95$ ,  $df = 1$ ,  $p = 0.16$ .

The probability that a prey item delivered at the nest was a bird when the previous prey delivered at the nest was a bird decreased with time since previous prey delivery (Figure 10).

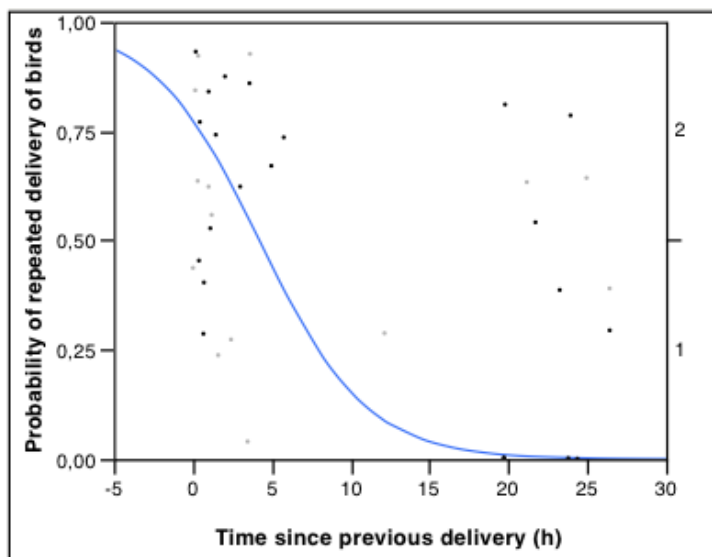


Figure 10. The probability that a prey item delivered at the eagle owl nest (N) was a bird when the previous prey item delivered (N-1) was a bird as a function of time since previous delivery, measured in hours (1 = bird, 2 = not bird). Whole model  $N = 14$ ,  $\chi^2 = 6.61$ ,  $df = 1$ ,  $p = 0.010$ .

Time since previous delivery of prey had no effect on the probability that the prey item delivered at the nest was the same prey as previous for mammals other than hare (Figure 11).

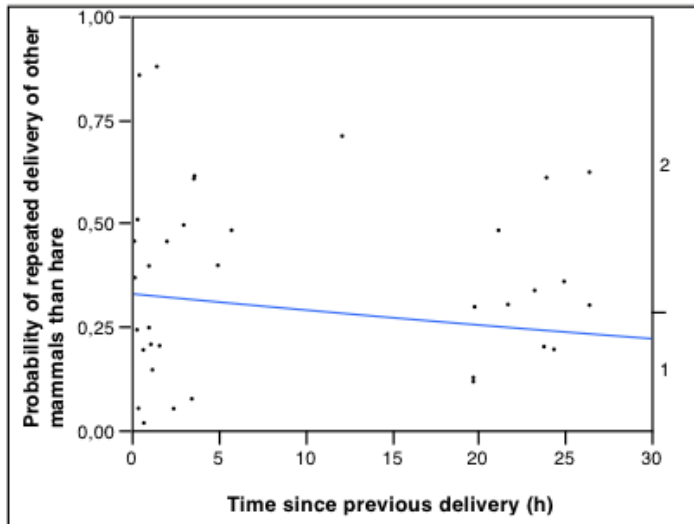


Figure 11. The probability that a prey item delivered at the eagle owl nest (N) was a mammal other than a hare when the previous prey item delivered (N-1) was a mammal other than a hare as a function of time since previous delivery, measured in hours (1 = mammal other than a hare, 2 = not other mammal than a hare). Whole model  $N = 7$ ,  $\chi^2 = 0.040$ ,  $df = 1$ ,  $p = 0.84$ .

## Prey handling before delivery

### Probability of decapitation

Because only birds were delivered decapitated, prey types other than birds were excluded from this analysis. The probability that a bird had been decapitated before delivery at the nest was significantly affected by deviation from solar midnight (Table 8). The probability of decapitation was negatively correlated with deviation from solar midnight, meaning that a bird was more likely to be delivered decapitated closer to solar midnight (Figure 12).

Table 8. Logistic regression model of significant effects on the probability that a bird had been decapitated before delivery at the eagle owl nest. Whole model  $N = 19$ ,  $\chi^2 = 6.16$ ,  $df = 1$ ,  $p = 0.013$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	2.348	1.548			
Deviation from solar midnight	-1.575	0.859	1	6.16	0.013

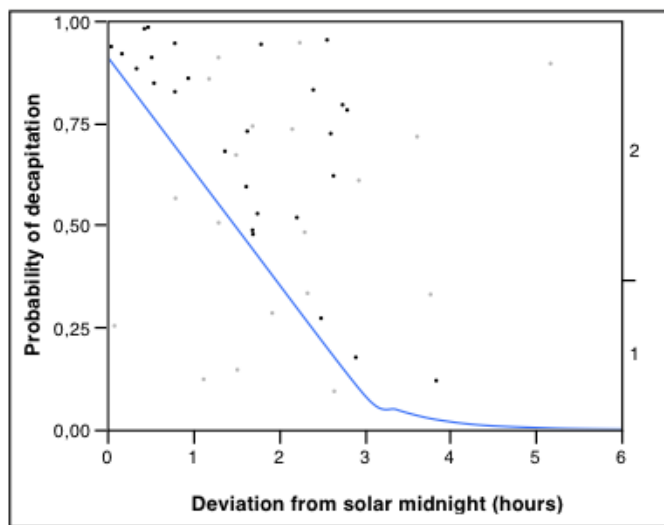


Figure 12. The probability that a bird had been decapitated before delivery at the eagle owl nest as a function of deviation from solar midnight (1 = decapitated, 2 = not decapitated). Whole model  $N = 19$ ,  $\chi^2 = 6.16$ ,  $df = 1$ ,  $p = 0.013$ .

## Prey handling at the nest

### Female feeding the nestling or nestling feeding unassisted

The probability that the female fed the nestling rather than the nestling fed unassisted decreased with age of the nestling (Figure 13) and increased with gross body mass of prey (Figure 14). The effects of these two explanatory variables on the probability that the female fed the nestling were examined in two separate models because of the instability in parameter estimates when including the two variables in the same model. The instability is most likely due to few cases of the female feeding the nestling.

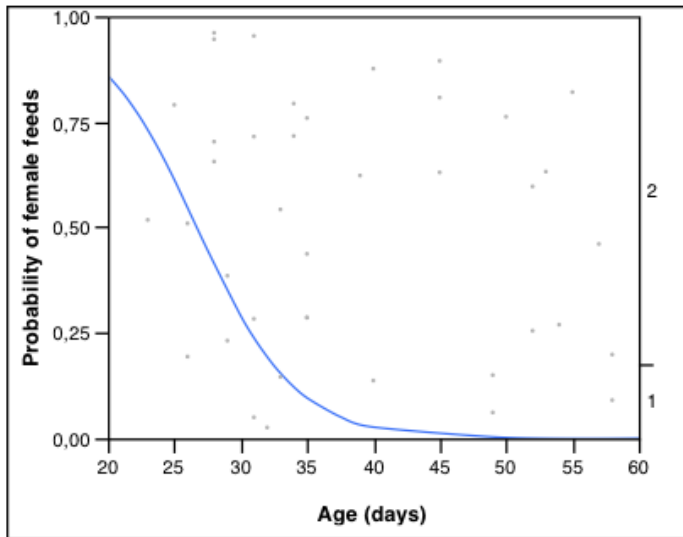


Figure 13. The probability that female eagle owl fed the nestling rather than the nestling fed unassisted as a function of age of the nestling (1 = female fed the nestling, 2 = nestling fed unassisted). Whole model  $N = 40$ ,  $\chi^2 = 11.49$ ,  $df = 1$ ,  $p = 0.0007$ .

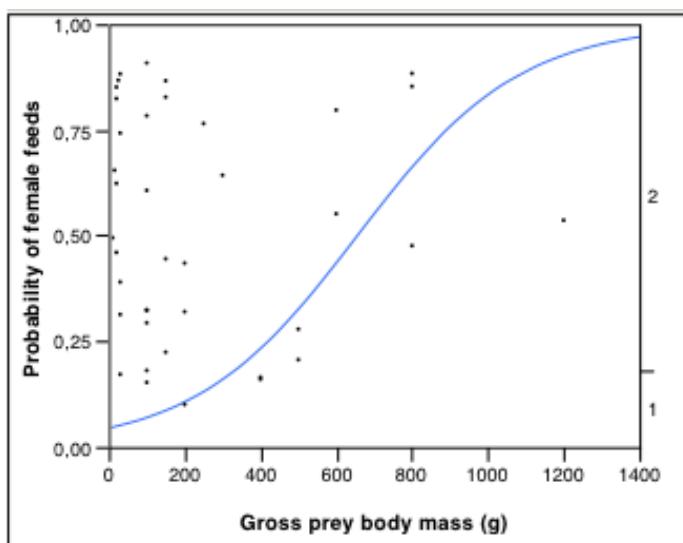


Figure 14. The probability that the female eagle owl fed the nestling rather than the nestling fed unassisted as a function of gross prey body mass (1 = female fed the nestling, 2 = nestling fed unassisted). Whole model  $N = 39$ ,  $\chi^2 = 10.13$ ,  $df = 1$ ,  $p = 0.0015$ .



## The probability of the nestling swallowing a prey item whole

The probability that the nestling swallowed a prey item whole decreased with increasing net body mass of the prey item (Table 9, Figure 15).

Table 9. Logistic regression model of significant effects on the probability of the nestling swallowing the prey item whole. Whole model  $N = 30$ ,  $\chi^2 = 13.12$ ,  $df = 1$ ,  $p = 0.0003$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	1.955	0.831			
Net body mass (g)	-0.016	0.007	1	13.12	0.0003

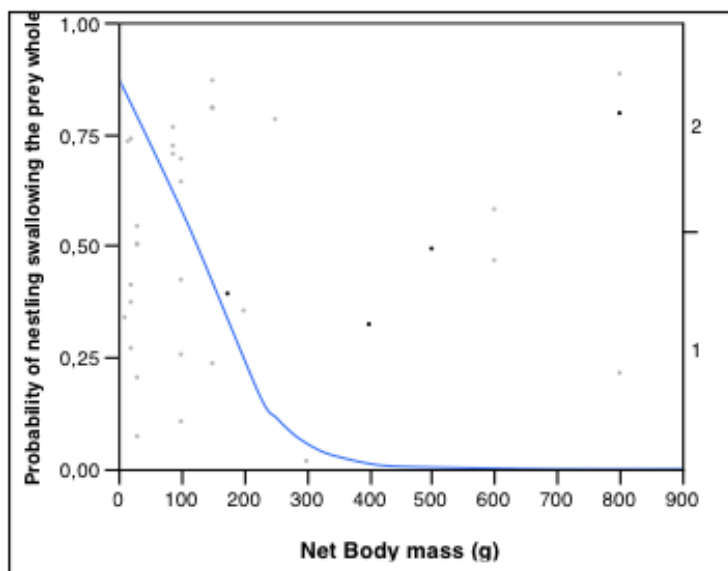


Figure 15. The probability that the nestling swallowed a prey item whole as a function of net body mass of the prey item (1 = nestling swallowed the prey whole, 2 = nestling did not swallow the prey whole). Whole model  $N = 30$ ,  $\chi^2 = 13.12$ ,  $df = 1$ ,  $p = 0.0003$

## Handling time

Net handling time was significantly affected by net body mass of prey (Table 10), and increased with increasing net body mass of the prey item (Figure 16).

Table 10. Generalized linear model (GLM) of significant effects on net handling time of a prey item ( $\log_{10}$  transformed). Whole model  $N = 36$ ,  $\chi^2 = 51.58$ ,  $df = 1$ ,  $p < 0.0001$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	- 1.651	0.419			
Net body mass ( $\log_{10}$ )	2.066	0.193	1	51.58	< 0.0001

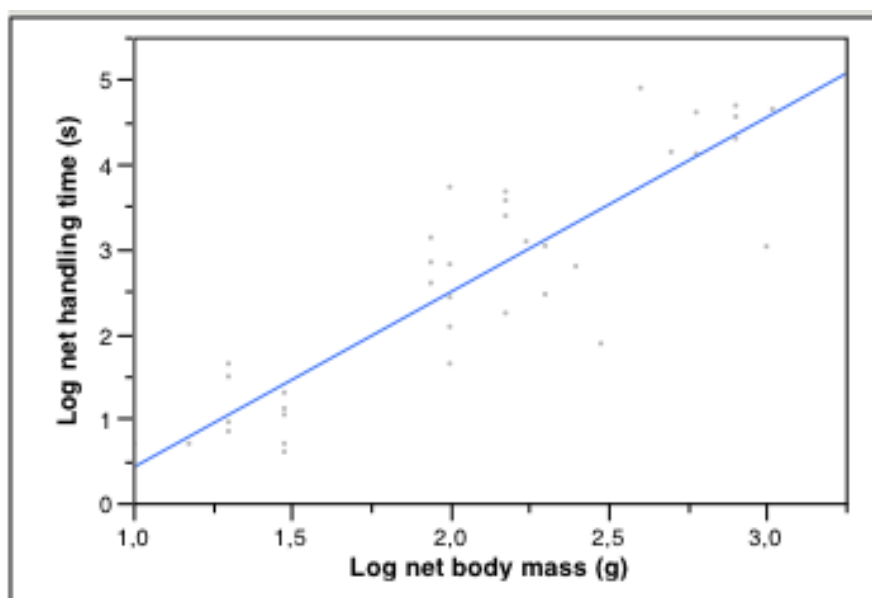


Figure 16. Net handling time of a prey item ( $\log_{10}$  transformed) as a function of net body mass of the prey item ( $\log_{10}$  transformed). Whole model  $N = 36$ ,  $\chi^2 = 51.58$ ,  $df = 1$ ,  $p < 0.0001$ .

To test if a long period of uninterrupted feeding was followed by a long pause and vice versa, I regressed the duration of the pause between two uninterrupted feedings on the previous uninterrupted feeding, as well the duration of uninterrupted feeding on the previous pause, for each of the 19 prey items with data on successive feedings and pauses. For the 19 regressions of the duration of a pause on the previous feeding the mean value of the slope was  $-0.40 (\pm 0.10)$ , with slope values ranging from  $-1.47$

to 0.18 (Figure 17 a). The slope values were significantly smaller than zero (matched pairs t-test, one tailed:  $N = 19$ ,  $t = 3.92$ ,  $df = 18$ ,  $p = 0.0005$ ). Thus, a long feeding unit was followed by a short pause unit. For the 19 regressions of the duration of a feeding unit on the previous pause unit the mean value of the slope was  $-0.53$  ( $\pm 0.24$ ), with slope values ranging from  $-4.21$  to  $0.24$  (Figure 17 b). Also here, the slope values were significantly smaller than zero (matched pairs t-test, one tailed:  $N = 19$ ,  $t = 2.17$ ,  $df = 18$ ,  $p = 0.022$ ). Thus, a long pause unit was followed by a short feeding unit.

There was no correlation between values of the slope and the number of units with feeding followed by a pause ( $N = 19$ ,  $R^2 = 0.10$ , F-ratio = 1.91,  $p = 0.19$ ) or between the slope and the number of units with a pause followed by a feeding ( $N = 19$ ,  $R^2 = 0.11$ , F-ratio = 2.06  $p = 0.17$ ).

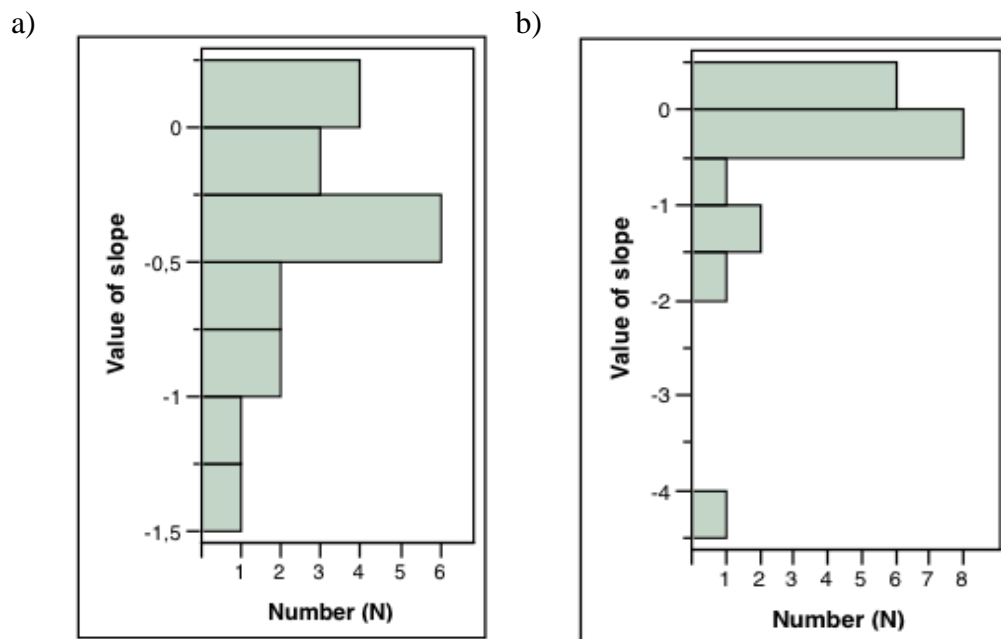


Figure 17. The distribution of the values of slopes when regressing a unit of pause time (no handling of prey) on the previous unit involving handling of prey (a), and when regressing a unit involving handling of prey on the previous unit of pause time (b).

## Number of meals per prey item

The number of meals per prey item was significantly affected by prey type (bird or mammal), net body mass of prey, and whether the female fed the nestling rather than the nestling fed unassisted (Table 11). Frog was excluded as a prey type in the model due to small sample size and the uncertain body mass, which was only an estimate from another study.

Number of meals per prey item increased with net body mass of prey (Table 11) and differed between prey types, and between feeding by the female and feeding by the nestling (Table 11). Number of meals per prey item increased with net body mass of prey. Number of meals was lower if the prey item was a bird than if the prey item was a mammal, and lower if the nestling fed unassisted than if the female fed the nestling (Table 11).

Table 11. Generalized linear model (GLM, Poisson regression) of significant effects on number of meals per prey item, with mammal and nestling fed unassisted as intercept for the variables prey type and female feed. Whole model  $N = 30$ ,  $\chi^2 = 97.88$ ,  $df = 3$ ,  $p < 0.0001$ .

Explanatory variables	Estimate	SE	df	$\chi^2$	p
Intercept	- 0.875	0.393		5.16	0.023
Prey type [1]	- 0.264	0.071	1	14.24	0.0002
Net body mass ( $\log_{10}$ )	0.669	0.157	1	18.96	< 0.0001
Female feeds [1]	0.406	0.080	1	24.78	< 0.0001

## Ingestion rate

There was no significant effect of gross body mass of prey delivered at the nest on the ingestion rate of prey when the female fed the nestling (Table 12). However, gross body mass of prey had a significant effect on the ingestion rate of prey when the nestling fed unassisted (Table 13). The ingestion rate decreased as the gross body mass of prey increased (Figure 18).

Table 12. Linear regression model of the effect of gross body mass of prey (g) ( $\log_{10}$  transformed) on the ingestion rate (g/min) ( $\log_{10}$  transformed) when the eagle owl female fed the nestling (N = 5,  $R^2 = 0.17$ ).

Explanatory variables	Estimate	SE	t	p
Intercept	2.186	2.505	0.87	0.447
Gross body mass ( $\log_{10}$ )	-0.729	0.918	- 0.79	0.485

Table 13. Linear regression model of the effect of gross body mass of prey (g) ( $\log_{10}$  transformed) on the ingestion rate (g/min) ( $\log_{10}$  transformed) when the eagle owl nestling fed unassisted (N = 30,  $R^2 = 0.50$ ).

Explanatory variables	Estimate	SE	t	p
Intercept	3.511	0.422	8.32	< 0.0001
Gross body mass ( $\log_{10}$ )	- 1.117	0.211	- 5.30	< 0.0001

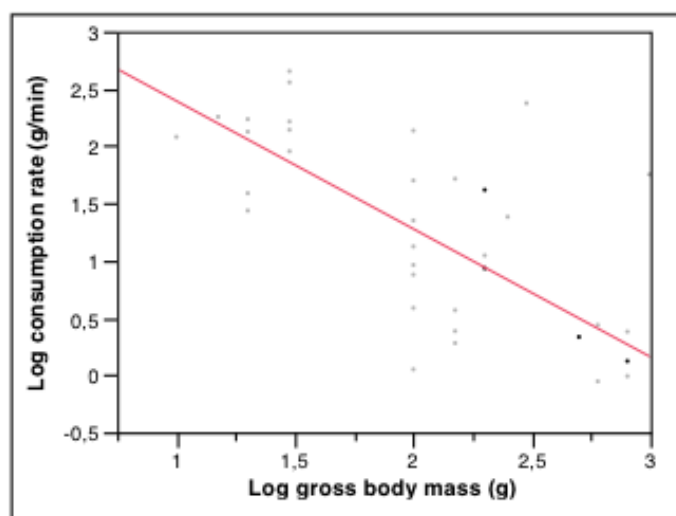


Figure 18. Linear regression model of ingestion rate in relation to gross body mass of prey when the eagle owl nestling fed unassisted (N = 30,  $R^2 = 0.50$ ).

## Discussion

### Prey delivered at the nest

A total of 51 prey items were recorded delivered at the eagle owl nest during the period of video monitoring, of which 47% were mammals, 39% were birds, and 8% were frogs. The remaining 6% of the prey items were not possible to identify to any taxonomic level. Mammal as the dominant prey type corresponds with some earlier studies from Norway and Sweden (Curry-Lindahl 1950; Hagen 1952; Mysterud & Dunker 1982), but not with the study by Willgoths (1974), where birds accounted for 64% of all the vertebrates and were the main category of prey items. These studies were based on collected prey remains and pellets. The head of a bird is easier to detect than intestines of mammals, thus an overestimation of birds may occur (Slagsvold et al. 2010). Mountain hare was the most abundant prey in my study, comprising 28% and 57% by number and mass, respectively. The large amount of mountain hare in the eagle owl's diet corresponds with earlier findings (Hagen 1952; Willgoths 1974).

The prey items recorded delivered at the nest in my study span widely in taxonomy and body size, with amphibians represented by the common frog, species of mammals ranging from small rodents to large mountain hares and birds ranging from small waders i.e. the common snipe to larger ones as the common raven. This confirms that the diet of the eagle owl consists of a great diversity of prey items (Curry-Lindahl 1950; Hagen 1952; Willgoths 1974; Mysterud & Dunker 1982; Cramp 1985). The composition of prey items delivered at an eagle owl's nest reflects the local fauna represented in the area, as the eagle owl captures the most abundant and easily captured prey (Curry-Lindahl 1950; Willgoths 1974). Thus, the diet of the eagle owl most likely will vary geographically and between different years as the habitat and prey availability differs from one area to another (Curry-Lindahl 1950; Willgoths 1974; Sàndor & Ionescu 2009).

A Swedish study conducted by Curry-Lindahl (1950) with metadata consisting of earlier findings of the eagle owl's diet across Sweden, found that the eagle owl's diet comprised of 55% mammals by number, with small rodents as the major part, consisting of as much as 42%. This was also the case in a study done by Willgoths

(1974) based on metadata of the eagle owl's diet across Norway, where small rodents accounted for 30% of the total of prey items by number. Thus, it seems that small rodents are important species of prey in the diet of the eagle owl. Nonetheless, in my study, small rodents only accounted for 18% by number of total prey items delivered at the nest. This may be due to the long period with relatively stable low populations of small rodents in the area, as found from registrations of small rodents in Lund, located approximately 80 km southeast of the study area, as a part of the TOV-project (Terrestrial Ecosystems Monitoring Program) conducted by the Norwegian Institute of Nature Research (NINA). There was a peak in the populations of small rodents in 2010 (Framstad 2011), and a low in 2011 and 2012 (Framstad 2012; Framstad 2013). According to a study from Finland (Korpimäki et al. 1990) where the diet of breeding eagle owls and Ural owls (*Strix uralensis*) was related to the abundance of small mammals as estimated from snap-trapping and of game species as derived from game questionnaires, the eagle owl took more game prey items when voles, which was their main prey type, were scarce. This may explain why the mountain hare, rather than small rodents, was the dominating prey type in my study.

As much as 35% by number of total prey items delivered at the nest in my study were related to wetland areas. Among the species delivered at the nest living in or near wetland areas were duckling, commons snipe, woodcock, shorebird, northern lapwing, water vole and common frog. Thus, wetlands located in the study area are of importance for the eagle owls as habitats for finding food. This corresponds with other findings from the same area, which suggested that the eagle owls preferred to remain close to water and bog areas during the breeding season, probably due to the large availability of prey in humid habitats (Oddane et al. 2012). Wetland areas have been found to be important habitats providing food for the eagle owl in other studies as well (Mysterud & Dunker 1982).

## **Hunting activity**

All prey items recorded delivered at the eagle owl nest were delivered within 9 hours from solar midnight, with the majority delivered within 4 hours from solar midnight. These results correspond with earlier findings showing that the eagle owl is a primarily nocturnal bird (Hagen 1952; Mysterud & Dunker 1982; Cramp 1985; Delgado & Penteriani 2007; Oddane og Undheim 2007). However, there are exceptions that contradict these findings and demonstrates that the eagle owl in some cases also delivers prey items at daytime, although the parents mainly provides the nestlings with food at night (Mysterud & Dunker 1982).

## **Prey selection**

The probability that a prey item delivered at the eagle owl nest was a hare increased as the delivery was closer to solar midnight. Hence, the darker, the more the eagle owl selectively hunted hares or succeeded in hunting hares. This fits the fact that mountain hares are primarily nocturnal and feed at night (Angerbjörn & Flux 1995). The probability that a prey item delivered at the nest was a hare also increased with increasing ambient temperature. A possible explanation may be that mountain hares may be more active when foraging on sprouting shoots of plants, which have an improved growth rate at higher temperatures, and thus the hares may be less vigilant and easier to capture.

The probability that a prey item delivered at the nest was a bird decreased throughout the evening and further after solar midnight throughout the morning. A possible explanation for this may be that birds are difficult prey to catch because they may escape by flying, and because flight is an energy demanding activity for the eagle owl and birds in general (McWilliams et al. 2004), the eagle owl cannot afford to spend that much of energy, and will focus on hunting the nocturnal mountain hares as its main prey species instead. There was also a higher probability that the eagle owls delivered a bird at the nest in the morning than in the evening. A likely explanation for this may be that the birds in general sing more actively in the morning than in the



evening (Slagsvold 1977), and thus they are easier to detect and capture for a potential predator like the eagle owl.

The probability that a prey delivered at the eagle owl nest was a mammal other than a hare increased with decreasing ambient temperature. A possible explanation for this may be that small mammals and rodents are alternative prey when mountain hares as the preferred prey type are scarce due to the low temperature. The probability that a prey item delivered at the nest was a mammal other than a hare also increased throughout the evening towards solar midnight and further increased from solar midnight towards the morning. Small mammals were thus taken by the eagle owl in an opposite pattern than the birds, and hence they were a mirror image of each other in relation to time of delivery. Due to the low abundance of small mammals among the prey items recorded delivered at the eagle owl nest, birds and hares may be compensating as prey types for the shortage in availability of small mammals. This was the case in a study from Finland, where the eagle owl took more small game species as an alternative prey when small rodents as their main food source were scarce (Korpimäki et al. 1990). However, the findings in my study should only be regarded as speculations as snap trapping of small mammals in the territory of the breeding pair of eagle owls was not done, and thus information on their prevalence in the area is limited.

The probability that a prey item delivered at the eagle owl nest was a frog increased with decreasing temperature. A possible explanation for this may be that it was raining when the frogs were delivered at the nest (pers. obs.), and therefore the temperature may have decreased. All frogs were delivered before solar midnight. However, this result should be treated with caution, as there were some technical difficulties causing disruptions in the video recordings the night when three of the four frogs recorded were delivered at the nest. This may have resulted in missed records of deliveries of frogs brought after solar midnight. The possible explanations presented here should be regarded with caution because parameter estimates in the statistical analyses were unstable.

## **Hunting strategy**

The probability that the eagle owl parents delivered a hare when the previous prey item they delivered was a hare, increased with time since previous prey delivery. A possible explanation may be that the mountain hares were relatively heavy compared to other species of prey delivered at the nest, except of a few birds, and therefore the parents did not need to deliver a new prey item in a while. Another explanation may be that the mountain hares were distributed over a large area, so when one hare was captured, the eagle owl would not necessarily find another one at the same place. Thus, it may benefit the eagle owl to return to the area after a while so that the remaining hares are not as vigilant as immediately after their last visit. The latter explanation was also suggested for willow grouse (*Lagopus lagopus*) as a species of prey for the golden eagle (*Aquila chrysaetos*) (Skouen 2012).

The probability that the prey item delivered at the nest was a bird when the previous prey item delivered was a bird, decreased with time since previous prey delivery. A possible explanation may be that the majority of the bird species delivered at the nest have a clumped distribution (Sonerud 1985), as this may in particular be the case for the waders which lives close to or in wetland areas and most likely are even more stationary in the breeding season. A win-stay hunting strategy involving returns to successful capture sites, in this case to wetland areas, would enable the eagle owls to capture more birds, because concentrated search in the same area where a prey was captured earlier improves the encounter rate (Sonerud 1985).

## **Prey handling before delivery**

Among the prey items recorded delivered at the eagle owl nest only birds had been decapitated. Of the birds delivered at the nest 35% had been decapitated. Other studies support this finding, with birds as a major category of prey decapitated prior to delivery (Rønning 2007; Steen et al. 2010; Skouen 2012). The swallowing threshold model presented by Kaspari (1990) proposes preparation of prey items too large to swallow as a way of preventing the limitation of gape size, which according to Slagsvold & Wiebe (2007) represents a feeding constraint. Thus the head of an avian

prey may be removed if too large or too risky to swallow due to the sharp bill (Steen et al 2010). However, the differentiated sex roles of the eagle owl, where the male provides most of the food early in the breeding season and the female feeds the nestlings by dividing the prey items into smaller parts (Cramp 1985), suggests that the swallowing constraint is not an issue for the eagle owl (Slagsvold & Sonerud 2007).

The probability that a bird delivered at the nest had been decapitated increased the closer to solar midnight the bird was delivered. Regardless of whether the bird was delivered in the evening or in the morning, it appears that the majority of the decapitated birds were delivered within a limit of 3 hours from solar midnight. A possible explanation for this may be that when it becomes darker, the parents can afford to decapitate and self-feed. A brain is nutritious and has a high fat content (Slagsvold et al. 2010), and because preparation of a prey item for the nestling is a cost for the parent due to lost time for self-foraging (Ponz et al. 1999) the parent can reduce time needed for self-foraging by consuming the most nutritious prey parts. Further, this would result in less prey mass to transport back to the nest for the parent and thus less energy used in flight (Sodhi 1992; Rands et al. 2000). This would be a useful way of conserving energy for a single prey loader like the eagle owl.

## **Prey handling at the nest**

### **Female feeding the nestling or nestling feeding unassisted**

The probability that the female fed the nestling increased with gross body mass of prey and decreased with age of the nestling. This was also the case for nestlings of Ural owls and golden eagles (Rønning 2007; Skouen 2010). The gape size limitation (Slagsvold & Wiebe 2007) seemed to prevent the nestling from swallowing larger prey items, and hence the female helped partition of the prey item if it was large and the nestling was young. Thus, it seems that the primary function of prey handling was to make the prey item small enough for ingesting (Sherry & McDade 1982). After the nestling exceeded an estimated age of 34 days, there was no evidence of the female feeding the nestling (pers. obs.). This is consistent with findings of eagle owl nestlings capable to partition prey items at an age of 6 weeks (Cramp 1985). At that

age, the nestling probably is better adapted morphologically to handle and partition larger prey items by itself (Marchetti & Price 1989; Steen 2004).

### **The probability of the nestling swallowing a prey item whole**

The probability that the nestling swallowed a prey item whole decreased as the net body mass of the prey item increased. Thus, there was a higher probability that the nestling swallowed the smaller prey items whole than the larger ones. This is in accordance with other studies (Steen 2004; Skouen 2012). A likely explanation for this may be that the gape size limitation (Slagsvold & Wiebe 2007) prevented the nestling from swallowing prey items with a large net body mass in one piece (Steen 2004).

### **Handling time**

Net handling time, i.e. the time the nestling spent at feeding when the pauses were subtracted, increased with an increasing net body mass of prey. This was also the case in earlier studies on handling time in birds (Sherry & McDade 1982; Steen 2004; Rønning 2007; Slagsvold & Sonerud 2007; Skouen 2012). More time was probably needed for preparation of prey exceeding the swallowing threshold (Kaspari 1990) due to larger body parts and bones as the body mass of prey increased (Slagsvold & Sonerud 2007).

To reveal whether the duration of each period of uninterrupted feeding was affected by the gastric fullness of the nestling, I tested if a long period with uninterrupted feeding was followed by a long pause. I expected that if the feeding time was influenced by gastric fullness, the nestling would need a longer pause for digestion of food before there was room for more food to be consumed. A long pause would then be followed by a long period of uninterrupted feeding due to a greater proportion of the stomach being empty and more time could be spent on digesting food. However, this was not the case. A long period of uninterrupted feeding was followed by a short pause, and a long pause was followed by a short period of uninterrupted feeding. A possible explanation for a long period of uninterrupted feeding followed by a short

pause may be that the food had low profitability due to the difficulty of handling larger prey items. Consequently the nestling ingested less food per time unit, and thus needed to spend more time on feeding and less time on pauses to obtain a certain level of nutrient required. A possible explanation of why a long pause unit was followed by a short feeding unit may be that the nestling was satiated, or that it tried to handle a prey that initially was too large to manage.

### **Number of meals per prey item**

Number of meals per prey item increased with net body mass of prey. The main reasons for this are most likely that the eagle owl nestling became satiated and had to divide larger prey item into several meals (Slagsvold et al. 2010), or because the eagle owl nestling had to divide the handling into several meals as the preparation of larger prey items was time and energy consuming due to larger bones and thicker skin (Slagsvold & Sonerud 2007).

Number of meals per prey item was lower if the prey item was a bird than if it was a mammal. A possible explanation may be that the hare was the only mammal that the eagle owl nestling consumed in more than one meal, and due to the relatively large body size of a hare it consists of a large amount of skin and bones (Slagsvold & Sonerud 2007), and thus it most likely was more difficult to ingest than a bird.

Number of meals per prey item was higher if the female fed the nestling rather than the nestling feeding unassisted. A possible explanation for this may be an increase in body mass causing an obstruction for the nestling so that it cannot utilize as much of the prey item as the female due to larger body parts, larger bones and thicker skin as mentioned earlier. Thus, the nestling may desert the prey item at an earlier stage than if the female fed the nestling, which would result in fewer meals.

## **Ingestion rate**

When the female fed the nestling, the gross body mass of prey had no effect on the ingestion rate of nestlings. This may be due to a small sample of observations of the female feeding the nestling. The gape size is limiting the nestling from ingesting larger parts of prey item (Slagsvold & Wiebe 2007), thus I expect the nestling to be more dependent on its mother for feeding at an earlier age. The video monitoring started when the nestling had an estimated age of 22 days, and hence I have probably missed most foraging units where the female fed the nestling.

When the nestling fed unassisted the ingestion rate decreased with increasing gross body mass of prey. This has also been found for raptors in captivity (Slagsvold & Sonerud 2007; Slagsvold et al. 2010; Steen 2010). The ingestion rate provides a measure of the effectiveness of feeding (Slagsvold et al. 2010), hence the eagle owl nestling was more efficient in handling smaller prey items. One explanation for this may be that the larger prey items are more difficult to ingest due to the thicker skin, larger skulls and larger body parts (Slagsvold & Sonerud 2007), and thus longer time is spent on preparation of prey, lowering the ingestion rate (Kaspari 1990). Slagsvold and Sonerud (2007) found that the ingestion rate was higher when small prey items were consumed in one piece, as done by an adult eagle owl when ingesting small rodents (Slagsvold et al. 2010). In my study the eagle owl nestling swallowed small rodents, small birds and frogs whole, which probably contributed to an increased ingestion rate. According to the ingestion rate hypothesis (Slagsvold & Sonerud 2007), one reason for reversed sexual size dimorphism, where the male is smaller than the female, may be that the male as the main food provider in the early phase of the nestling period is able to catch smaller and more profitable prey items for the nestlings.

## **Limitations of video recording as method**

By studying the diet composition of a predator in the breeding season, the data are easier to collect, as the activity is concentrated around the nesting site (Lewis et al. 2004). To investigate prey delivery and diet of different species of birds, video monitoring seems to be the method that gives the most representative measure of the diet, with the smallest amount of unidentified prey items (Simmons et al. 1991; Lewis et al. 2004; Selås et al. 2007; Homme 2008; Steen et al. 2011b). By video monitoring as method one can also obtain supplementary details, i.e. the exact time of delivery and the handling of prey (Homme 2008).

However, there are several limitations of video monitoring as method. Technical failures which may occur are interruptions of the recordings due to power shortage in the batteries and lack of space on the memory cards, which may cause potential deliveries to be lost (Homme 2008; pers. obs.). Some biological constraints may also interrupt or affect the determination of species delivered to the nests, i.e. that nestlings turn their back to the camera or walk out of range of the camera lens (pers. obs.). The latter is common for eagle owl nestlings as they become older (Cramp 1985), and hence deliveries of prey may be lost.

Collecting and analyzing of prey remains as a method to investigate the diet of the eagle owl has been shown to overestimate the occurrence of larger prey, underestimate the occurrence of mammals, and overestimate the occurrence of birds in the diet (Sergio 2002). Overestimating the occurrence of avian prey when determining diets of raptors based on prey remains have also been found in other studies regarding comparison of methods used for diet determination (Simmons et al. 1991; Lewis et al. 2004; Selås et al. 2007). Pellets have found to overestimate the occurrence of mammals as prey, and underestimate the proportion of birds (Simmons et al. 1991). Homme (2008) recommended video recording as a method to correct for biases when using pellets and prey remains as methods for studying diet composition in raptors, and concluded that the latter traditional methods were necessary to include in order to identify prey species difficult to identify from video recordings (Homme 2008).

## Conclusion

By video monitoring at an eagle owl nest in the breeding season, diet composition and handling of prey was investigated. Mammals turned out to be the major prey type, with the mountain hare as the dominating prey species both by number and mass. Shorebirds were an important part of the eagle owl's diet, and thus wetland areas seem to be important habitats for the eagle owls in my study area. The female fed the nestling and partitioned the larger prey items during the first weeks of the nestling period to prevent the gape size from being a feeding constraint. This supports the hypothesis suggested by Slagsvold & Sonerud (2007) for reversed sexual size dimorphism (RSD) in raptors, that the male is smaller than the female to be able to provide the nestling with smaller prey, which in this study turned out to be the most profitable prey size if the aim was to maximize the ingestion rate. The use of video monitoring as a method to provide detailed information about the eagle owl's diet and handling of prey gives a complete description of the diet because the prey items are identified precisely. However, additional studies from several successive years together with measures of the prey availability in the eagle owl's territory, as well as data from additional nests containing more than one young is needed to determine the trends presented in this study with more certainty.



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