Acknowledgements

Abstract

The diet and handling of prey in breeding golden eagles (*Aquila chrysaetos*) was studied by video monitoring one nest in southern Norway in a year of peak vole (Cricetidae) population and low willow grouse (*Lagopus lagopus*) population, from the nestlings were c. 10 days old until fledging. Handling time was determined for different prey types and prey sizes when the female fed the nestlings and when the nestlings fed unassisted. A total of 181 prey items were recorded delivered. In total 70% of all prey items delivered at the nest were birds and 30% were mammals. The most important prey type was willow grouse, both by numbers (34%) and by mass (35%). Mountain hare (*Lepus timidus*) and red fox (*Vulpes vulpes*) made up 7% and 3%, respectively, by numbers, and 33% and 14%, respectively, by mass. Thrushes (*Turdus* sp.) (24%), *Microtus* voles (11%) and lemming (*Lemmus lemmus*) (9%) were also important numerically as prey in the breeding diet of the eagles. No ungulates were observed delivered at the nest. The male golden eagle delivered the majority of prey (68%) to the nest and he mainly delivered birds (80%). The probability of delivering a willow grouse at the nest decreased throughout the season. The eagles appeared to adjust hunting strategy to prey species, and willow grouse was most likely hunted by using a win-shift strategy while thrushes were more likely to be hunted with a win-stay strategy. Preparation of prey prior to delivery at the nest (plucking or partitioning) was more likely for avian than for mammalian prey, and also for larger prey, but less likely with increasing age of the nestlings. Further preparation in the nest by plucking of prey before feeding was more likely to be preformed by the female rather than by the nestlings. Handling time was longer for mammalian than for avian prey and increased with body mass of the prey, both when the female fed the nestlings and when the nestlings ingested prey unassisted. To explain prey selection there is still a need for assessing handling efficiency of different prey.

Sammendrag

Kongeørnens (*Aquila chrysaetos*) diett i hekkeperioden og håndtering av byttedyr ble undersøkt ved videoovervåking i et kongeørnreir i Sør-Norge i et toppår for bestand av smågnagere (Cricetidae) og lav bestand av lirype (*Lagopus lagopus*), fra ungene var ca. 10 dager gamle til de var flygedyktige. Håndteringstid ble bestemt for ulike byttedyrtyper og størrelser på byttedyr, både for når hunnen foret ungene og når ungene spiste selvstendig. Totalt 181 byttedyr ble registrert. Av alle byttedyr registrert levert på reiret var 70 % fugl og 30 % pattedyr. Lirype utpekte seg som det viktigste byttedyret både i antall (34 %) og biomasse (35 %). Hare (*Lepus timidus*) og rødrev (*Vulpes vulpes*) utgjorde henholdsvis 7 % og 3 % av antallet, og henholdsvis 33 % og 14 % av biomassen. Trost (*Turdus* sp.) (24 %), *Microtus* gnagere (11 %) og lemen (*Lemmus lemmus*) (9 %) og var også viktige i antall i dietten til de hekkende kongeørnene. Ingen klovdyr ble registrert levert på reiret i løpet av overvåkingsperioden. Kongeørn hannen leverte flest byttedyr i løpet av hekkeperioden (68 %), og flesteparten av byttedyrene han leverte var fugl (80 %). Sannsynligheten for å levere lirype på reiret minket gjennom sesongen. Kongeørnen skiftet tilsynelatende jaktstrategi ut i fra byttedyr art, og lirype ble sannsynligvis jaktet ved bruk av en "win-shift" strategi mens trost sannsynligvis ble jaktet ved bruk av "win-stay". Preparering av bytte før levering på reiret (ribbing eller partering) var mer sannsynlig for fugl som bytte enn for pattedyr, og var også mer sannsynlig for større byttedyr, men mindre sannsynlig med økende alder på kongeørn ungene. Videre preparering av bytte i reiret ved ribbing før spising var mer sannsynlig å bli utført av hunnen enn av ungene. Håndteringstid var lengre for pattedyr som bytte enn fugl og økte også med økende biomasse hos byttedyret, både for når hunnen foret ungene og når ungene spiste selvstendig. For å kunne forklare seleksjon av byttedyr er det fremdeles et behov for å ta for seg håndteringseffektivitet av ulike byttedyr.

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Introduction

According to optimal foraging theory, a predator should maximize its net rate of energy intake, and thus selectively hunt some species and avoid others (Barnard 2004). Whether less profitable prey should be hunted will depend on the availability of preferred prey. The profitability of a prey will depend on both its energetic value and the time spent handling it (Barnard 2004). Handling time is defined as the time spent capturing, preparing and ingesting a prey item (Kaspari 1990). Preparation of a prey will be the time and energy a predator spends modifying its prey before consumption, for example by removal of inedible or less preferred parts of the prey. Raptors have evolved to catch prey with their feet and to use the bill as a tool to tear a prey into pieces before ingesting, and for this reason raptor meals are often extended and time consuming (Slagsvold & Sonerud 2007). Handling of prey should thus be efficient. In particular, efficient handling would be of utmost importance when raptors are provisioning young, and morsels torn of the prey must be small to fit the gape size limit of the nestlings at the given age (Steen et al. 2010). Hence, time spent feeding are even more extended during the nestling period. Few quantitative studies of prey handling in raptors exist despite the fact that such knowledge is essential for understanding prey selection and foraging behaviour. Also, knowledge about how a predator´s diet changes in response to prey availability is key to understand the predator´s role in the ecosystem (Watson 2010).

The golden eagle (*Aquila chrysaetos*) is a large raptor with a widespread distribution ranging the northern hemisphere, and is adapted to a number of different habitats (Watson 2010). The presence of open, mountainous landscapes is a corporate element in its natural environment and is highly linked to its hunting of prey (Watson 2010). The diet of the golden eagle has been assessed in several studies (Tjernberg 1981; Nyström et al. 2006; Watson 2010), which have shown that this large avian raptor is a highly opportunistic hunter with a diverse diet (Watson 2010). Medium-sized birds and mammals, such as grouse (i.e. willow grouse (*Lagopus lagopus*), rock ptarmigan (*Lagopus mutus*), black grouse (*Tetrao tetrix*), capercaillie (*Tetrao urogallus*)) and lagomorphs (i.e. mountain hare (*Lepus timidus*)), are major prey groups, typically ranging in body mass from 0.5-4.0 kg (Watson 2010). Several studies however show that ungulates, especially reindeer (*Rangifer tarandus*), also compose an important part of the diet of golden eagles (Tjernberg 1981; Nybakk et al. 1999; Pedrini & Fabrizio 2001; Valkenburg et al. 2004; Norberg et al. 2006; Nyström et al. 2006). This usually encompass fawns and lambs of domestic reindeer and sheep (*Ovis aries*), but some

studies have documented predation on adult domestic reindeer (Nybakk et al. 1999) and adult sheep (Bergo 1987; Warren et al. 2001), showing golden eagles capable of hunting and killing mammals weighing more than 30 kg (Bergo 1987; Nybakk et al. 1999; Norberg et al. 2006). As much as c. 10% of the diet of golden eagles have been found to consist of reindeer (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007). Thus, there is still controversy about the importance of golden eagles as a predator on livestock in Norway. Every year the Norwegian government pay large sums to reindeer owners and sheep owners as compensation for the loss of livestock due to predation from this predator (Gjershaug & Nygård 2003).

So far, most studies on the diet of golden eagles have been done by indirect methods analysing prey remains and regurgitated food pellets found at the nest sites at the end of a breeding season (Tjernberg 1981; Collopy 1983; Pedrini & Fabrizio 2001; Seguin et al. 2001; Nyström et al. 2006; Johnsen et al. 2007). The quality of prey remains and pellets are dependent on prey size and prey characteristics, e.g. bill or claws (Tornberg & Reif 2007), environmental conditions and how well the golden eagle pair cleans out the nest (Tjernberg 1981; Seguin et al. 1998). Indirect methods of diet analysis may lead to misinterpretation of the importance of groups of prey in the diet, with typical overestimation of larger prey and birds, and underestimation of smaller prey items (Tjernberg 1981; Collopy 1983; Seguin et al. 1998; Sveen 2006; Tornberg & Reif 2007; Homme 2008; Sanchez-Zapata et al. 2010; Slagsvold et al. 2010). The use of direct methods to analyse the diet of golden eagles has mainly consisted of observing from a blind (Collopy 1983), which is a very time consuming task. However, studies conducted in Japan on prey composition of the golden eagle have used direct observations with photographs and video recordings at a distance from the nest (Takeuchi et al. 2006).

In this study I investigated prey composition of a golden eagle pair in a mountainous region in southern Norway by using direct observations from video recording at the nests. First, I wanted to analyse the importance of different groups of prey in the diet during the breeding season. In particular I wanted to address the importance of ungulates in the diet of the golden eagles. The largest of the last remaining wild reindeer herds in Norway has its home range within the territories of the golden eagle population in my study area. Furthermore domestic sheep and lambs are released on summer grazing in the mountainous area in and around the golden eagle territories every year. Second, I wanted to analyse prey handling and parental behaviour of the eagles at the nest. Handling of prey may vary with prey type and prey size,

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as well as with age of the nestlings, in terms of the female feeding dependent nestlings or the nestlings ingesting prey unassisted. In golden eagles, as in most raptors, the male provides most of the food for the female and the nestlings during the nestling period (Watson 2010), so I also wanted to analyse parental roles in relation to prey delivered at the nest. To my knowledge a video camera has never before been installed at the nest of a breeding pair of golden eagles. This would offer a unique opportunity to analyse the diet of the golden eagle in more detail, as well as observing behaviour of the parents and nestlings and handling of prey at the nest.

Methods

Study area and study species

The study was conducted in June–July 2011 in Tinn Municipality in Telemark County, in southern Norway (66°40´- 66°60´ N; 11°50´ - 14°00´ E). The study area is part of the eastern Hardangervidda mountain plateau and covers c. 100 km², with altitude varying from c. 900–1300 m above sea level. The vegetation is sparse, with patches of bogs and with numerous lakes. The lake Møsvatn lies west of the study area, and the lake Tinnsjø is situated east. There are several steep valleys surrounding the mountainous high land, and the study area is situated in one of these valleys. The vegetation here is lush and species rich with tall-herb woodland consisting mainly of downy birch (*Betula pubescens*) forest, blending in with some Norway spruce (*Picea abies*). Shrubs of willow (*Salix* sp.) and mountain birch (*Betula pubescens ssp. czerepanovii*) become more dominating closer to the tree line at c. 1000 m above sea level. The area has been held as pastures and used as a grazing area for livestock in the past centuries (Geirsta, G. pers. comm.), but today the area is mainly used as grazing area for sheep during summer.

There are about 10 golden eagle territories (breeding pairs) in the area close to Møsvatn (*TOV, Direktoratet for naturforvaltning* 2009; Framstad 2011). In this study I video monitored prey deliveries at a nest in one of these territories for about seven weeks. The golden eagle is highly territorial (Newton 1979; Watson 2010) so I assumed that the female and male at the nest were the same individuals throughout the filming period. The nest was situated on a broad ledge in a mountainside facing south, and the camera was wedged in a crack in the mountainside above the nest. The video camera was installed at the nest site in autumn 2010 to minimize disturbance and to habituate the eagles to the camera. At this time of year the nestlings of the season abandon the territory of the parents, and the parents start to clean out the nest for the next breeding season (Watson 2010).

Prey availability

The Norwegian Institute for Nature Research (NINA) has a field station located at Møsvatn where registrations of birds, small mammals and vegetation are done every year as a part of the TOV-project (Terrestrial Ecosystems Monitoring Program) (Framstad 2011). Population

indices of willow grouse and voles (Cricetidae) in autumn have been used as predictors of the breeding success for golden eagles and gyrfalcons (*Falco rusticolus*) in the succeeding year (Framstad 2011). In 2010, the snap trapping of voles indicated that there was a medium dense population, which was also the case for several of the other TOV-areas in Norway (Framstad 2011). In 2011, the population index of voles at Møsvatn was even higher than the preceding year (E. Framstad, unpubl. data). Monitoring of willow grouse in 2010 revealed a slight decline in population size and production of young compared to 2009, and was amongst the lowest number of observations registered between 1992–2010, indicating a small population of willow grouse in the area (Framstad 2011). This was also the case in 2011 (E. Framstad, unpubl. data). For passerine birds there was also a slight decline in numbers of observed birds at the census points from 2009 to 2010 (Framstad 2011). Thus, during my study the vole population was relatively high, while the willow grouse population was relatively low.

Within the territory of the breeding golden eagles there are sheep grazing during summer. The wild reindeer herd of Hardangervidda also has part of its range within the territory, and there is a possibility that these areas are used as natal areas in spring (*Hardangervidda villrein - kalvingsområder* 2009). Hence, also ungulates were available as prey for the golden eagles.

Video monitoring

The filming started when the last hatched nestling was 7–10 days old. There were two nestlings in the brood. The filming lasted for 52 days, of which approximately thirteen days of recording failed. Out of 1248 hours of filming 316 hours were lost due to technical failure, resulting in 932 hours of video recording in total. The methods used for filming were the same as listed by Steen (2009). I used a CCD (charged-coupled device) camera equipped with a wide-angle lens to cover the whole nest bed. Frame rate was 10 pictures per s and resolution was set at 704 x 560 lines. The camera had IR-light for filming 24 h sessions. The camera was connected to a mini digital video recorder (mini DVR) with a 50 m long video cable, and placed in a waterproof plastic container. The mini DVR stored data on SD-cards and the container was placed in a hide on the ground away from the nest. In this way the monitoring and recording of prey deliveries and nest behaviour could be done with minimal disturbance to the eagles. The SD-card stored 32 GB of data and was replaced with a new SD-card every 5–7 days. The data were transferred to a laptop with an SD-card reader. To ensure continuous

recording I used two SD-cards of 32 GB. I viewed a sample of the recordings to check that the video equipment was working satisfactory. This process only took a couple of minutes to execute. A sealed 12 V DC lead battery (80Ah) supplied the mini DVR with power. In addition I used a 55 W solar cell panel coupled to the 12 V DC lead battery to charge the battery and also to supply the mini DVR with power. In this way I only had to replace the 12 V lead battery once during the period of filming. The solar cell panel charged with > 16 V.

A motion sensor was used to record prey deliveries and prey handling at the nest. To prevent the recorder from starting filming leaves blowing in the wind and other disturbing elements outside the nest, a masking tool was used to select the detection area. The detection area was set to the nest and the area close to the edge of the nest. A parent approaching by air would still trigger the sensor so that each prey delivery could be recorded. The sensitivity of the sensor was set to 12%. In this way minor movements from the nestlings would not be sufficient to trigger the sensor. The sensor was set to record for 10 s when triggered so that parenting behaviour and handling of prey could be recorded. The time of day was recorded whenever the camera was filming so that the exact time of each prey delivery could be used for analysis of the hunting patterns of the golden eagles. In addition I recorded continuously for 24 hours over a period of three days to test for default in the motion sensor. For further details of the video equipment, see Steen (2009). Data on temperature and precipitation during the period of filming was obtained from Møsstrand II weather station, where temperature was logged four times a day, and precipitation twice a day.

Prey delivery and feeding behaviour

All prey items recorded delivered at the nest by the golden eagles were identified to the lowest taxonomic level possible, and categorized into two main categories; birds or mammals. Each prey delivery was displayed on a projector and played frame by frame. Most prey items were identified to species or genus. The sex of the delivering parent was determined by morphological features and registered at each delivery. Time of arrival by the delivering parent was recorded, and also whether the prey item was complete, what part of the prey item was missing and whether it was plucked before delivery. Body mass for each prey species or prey type was obtained from literature (Cramp 1988; Cramp & Perrins 1993a; Cramp & Perrins 1993b; Cramp & Perrins 1994a; Cramp & Perrins 1994b; Frislid & Jensen 2004).

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When estimating body mass of decapitated voles and lemmings (*Lemmus lemmus*), I excluded 16.5% of the total body mass, based on data from Asakskogen (2003). When estimating body mass of decapitated birds, I excluded 12.9% of the total body mass, based on data from feeding behaviour of raptors in captivity (T. Slagsvold & G. A. Sonerud, unpublished data). For incomplete mammalian prey items like red fox (*Vulpes vulpes*) and mountain hare I excluded 20% of the total body mass if the prey item was decapitated, an additional 10% if front legs were missing, and an additional 20% if the front part of the prey item was missing as well. Hence, for prey items where much of the body was missing, I excluded 50% of the total body mass. I also recorded whether a prey item delivered at the nest (n) was the same prey species or prey type as the previous item (n-1), to test whether the eagles used a win-stay hunting strategy where the predator either focuses on a specific prey type or returns to the location where it captured the prey (Sonerud 1985; Barnard 2004).

I estimated the handling time for each prey item delivered at the nest (measured to the nearest s), both when the female assisted the nestlings in feeding and when the nestlings fed unassisted. According to Watson (2010) the female feeds dependent nestlings for the first 30 days of the nestling period. I used the same definitions of handling time as used by Steen (2010) on the Eurasian kestrel (*Falco tinnunculus*). Handling time was defined as the time that elapsed from the female bent her head down to tear off the first piece of the prey item until the item had been completely consumed or abandoned (Steen 2010). If the nestlings were old enough to feed unassisted they would show mantle behaviour and protect the prey item from the other sibling, or the siblings would share the item. I then defined handling time as the time that elapsed from the nestling first bent its head down to tear off the first piece of the prey item until the item had been completely consumed or abandoned (Steen 2010). The nestling would also swallow some prey items whole and handling time was then defined as the time that elapsed from the nestling first bent down its head to pick up the prey until its swallowing movements ended (Steen 2010). Time spent plucking the prey item was also registered as handling time. I defined plucking time as time elapsed from the female or nestling first bent down its head to tear off the first piece of the prey item until plucking of prey ended. Number of plucks was also recorded. Time spent feeding and plucking the prey item was then summarized to handling time. If the feeding or plucking session stopped for more than 5 s, I excluded this pause from the handling time. Cleaning after a feeding was not included in handling time, nor accounted for. Cleaning was defined as from when the female or nestlings started to pick up spilled leftovers of a prey item after a feeding. The reason why

this was excluded was that it was no longer possible to distinguish which prey item the female or nestlings was feeding from. By definition, handling time also includes time spent capturing and preparing a prey item prior to delivery, but this was not accounted due to difficulties in observing the golden eagles outside the nest. For 17 of the 181 prey items delivered at the nest, handling time was not obtained due to recording error, difficulties in registering feeding of the prey item or that the prey item was never eaten.

Due to error in the motion sensor some of the feeding and plucking sessions were not completely recorded. I therefore categorised the feeding and plucking sessions into four categories: 1) Complete recording. 2) Recording with exact start and stop time of handling of prey, but with one or several cuts in timeline in between. This could overestimate the time spent feeding or plucking, because some pauses longer than 5 s may not have been detected. 3) Recording where either start or stop time or both were missing. In these cases a maximum and minimum time was used. Maximum time spent handling the prey item was defined at the start of the session as the time at the last recording before a cut in timeline, and where the next recording displayed either the female or the nestlings feeding of or plucking the prey item. At the end of the feeding or plucking session maximum time was set at the next recording after the previous recording where the female or nestlings had been feeding or plucking the prey item. Minimum time spent handling the prey item was defined at the start of the session as the time at the recording where the female or the nestlings was feeding of or plucking the prey item. At the end of the session minimum time was set at the last recording before the next recording displayed the female or nestlings finished with feeding or plucking the prey. All pauses of more then 5 s were excluded, and I used the mean of the maximum and minimum time as the handling time of the prey item. 4) Recording where only maximum or minimum time was set due to an extended cut in timeline. This category consisted of the most insecure set of data and was therefore included in the analysis to control for measuring error.

If the female or nestlings had a pause longer than five minutes during feeding or a plucking session, the session was recorded as two different bouts (meals). Nestlings had to feed unassisted in all bouts to be assigned handling of a prey item unassisted. If the female fed the nestlings in one or more bouts handling time of the prey item would be recorded for the female. For most of the prey items the handling consisted of more than one bout and each bout was placed in one of the four categories. When summarizing the bouts the handling time could therefore consist of different categories (1–4). For bouts consisting of only category 1),

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handling time would also be categorised as 1). For bouts however, consisting of category 1) and one or more of category 2), handling time would be categorised as 2). For bouts consisting of one or more of category 3), handling time would be categorised as 3). This was done to correct for monitoring error.

Statistical analysis

All statistical analyses, as well as the construction of figures, were performed with the software JMP® version 9.0.0 (SAS 2010). The standard criterion of statistical significance was $\alpha = 0.05$. All residuals were checked for normality. Contingency analysis was used to test for association between prey type (bird or mammal) and the delivering sex (male or female). Logistic regression by likelihood ratio tests was used to test the effects of different variables on the probability that the delivering sex was male or female, whether a prey item delivered at the nest was a willow grouse, whether ambient temperature affected the delivery of willow grouse during the day, whether the current delivered prey item (N) was the same species as the previous prey item (N-1), whether the current delivered prey item was a willow grouse when the previous prey was a willow grouse, and whether the current delivered prey was a thrush when the previous prey was a thrush, whether a prey item was plucked, decapitated or partitioned before delivery at the nest (complete or not complete), whether the female or the nestlings handled the prey, and whether a prey item was monopolized by one of the nestlings.

The explanatory variables on whether the prey was delivered by male or female and whether a prey was complete when delivered at the nest were prey type (bird or mammal), body mass of the prey item before capture, age of the nestlings, and all interactions between the variables. The explanatory variables on whether the female or the nestlings handled the prey, and whether a prey item was monopolized by one of the nestlings were prey type (bird or mammal), net body mass of the prey item when delivered at the nest, age of the nestlings, and all interactions between the variables. The explanatory variables on the probability that a prey item delivered at the nest was a willow grouse were time since midday, whether the delivery was before or after midday, ambient temperature, age of the nestlings as a proxy for season effects, and all interactions between the variables. The explanatory variables on the probability that the current delivered species was the same as the previous prey item delivered were time since last delivery, change in date, prey body mass, age of the nestlings reflecting

season, and all interactions between the variables. The explanatory variables on the probability that the current delivered prey was a willow grouse when the previous prey item was a willow grouse, and the probability that the current delivered prey was a thrush when the previous prey item delivered was a thrush were time since last delivery, change in date, age of the nestlings and all interactions between the variables.

Because of non-normal distributed residuals, I used generalized linear models (GLM) with a Poisson error distribution and a log link to test for all possible effects of the different explanatory variables on handling time of prey, both when the female fed the nestlings and when nestlings fed unassisted, and number of meals per prey item when the female fed the nestlings and when the nestlings fed unassisted. The explanatory variables for number of meals per prey item for both female and nestlings were prey type (bird or mammal), body mass of prey, age of the nestlings, and all interactions between the variables. For handling time feeding categories 1–4 was used as an explanatory variable as well to correct for monitoring error.

Results

Prey selection

Prey delivered at the nest

A total of 181 prey items were recorded delivered at the golden eagle nest during the video monitoring, of which 111 items were identified to species level and another 63 to genus. Seven birds were not possible to identify to either species or genus (Table 1). In total 69.5% of all prey items were birds and 30.5% were mammals (Table 1). Willow grouse was the most common prey both by number and body mass, comprising 34.3% and 34.7%, respectively (Table 1). Thrushes were also numerous as prey by number, making them the second largest group of prey and comprising 24.3% of all recorded prey items delivered, but they made up only 4.9% of prey mass delivered. Mountain hare and red fox comprised 7.2% and 3.3% of prey by number, respectively, but no less than 33.0% and 13.7% of total estimated prey mass, respectively, making them the second and third most important group by prey mass delivered (Table 1). Lemming and *Microtus* voles also made up a large amount by number of the recorded prey items delivered at the nest, with 8.8% and 10.5%, respectively, but they made up only 0.9% and 1.0% of prey mass delivered, respectively (Table 1). Only three individuals (1.7% of prey by number and 3.9% by prey mass) of black grouse were recorded delivered at the nest (Table 1). No reindeer or sheep were recorded delivered at the nest during the period of video monitoring.

Table 1. Prey delivered at a golden eagle nest as recorded by video monitoring, given as percentage by number and percentage by body mass of each prey category.

Prey category	Prey number		Prey mass	
	N	%	Estimated body mass (g)	% of total estimated mass
Willow grouse (*Lagopus lagopus*)	62	34.3	500	34.7
Black grouse (*Tetrao tetrix*)	3	1.7	1167[1]	3.9
Whimbrel (*Numenius phaeopus*)	3	1.7	400	1.3
Woodcock (*Scolopax minor*)	1	0.6	300	0.3
Hooded crow (*Corvus cornix*)	1	0.6	500	0.6
Greenshank (*Tringa nebularia*)	1	0.6	200	0.2
Goshawk (*Accipiter gentilis*)	1	0.6	500	0.6
Fieldfare (*Turdus pilaris*)	2	1.1	100	0.2
Thrush indet. (*Turdus* sp.)	42	23.2	100	4.7
Duck indet. (Anatidae)	1	0.6	700	0.8
Warbler (Phylloscopidae)	1	0.6	10	0.01
Birds indet.	7	3.9	329[2]	2.6
Mountain hare (*Lepus timidus*)	13	7.2	2269[3]	33.0
Red fox (*Vulpes vulpes*)	6	3.3	2033[4]	13.7
Mink (*Mustela vison*)	2	1.1	600	1.3
Lemming (*Lemmus lemmus*)	16	8.8	50	0.9
Field vole or Root vole (*Microtus* sp.)	4	2.2	50	0.2
Vole indet. (Microtinae sp.)	15	8.3	50	0.8
Total	181	100.4	89 260	99.81

[1] Mean estimate, variation 900–1300 g

[2] Mean estimate, variation 100–500 g

[3] Mean estimate, variation 1000–3000 g

[4] Mean estimate, variation 2000–2200 g

The delivering sex

The sex of the delivering parent was determined for 162 of the 181 prey items delivered at the nest. The male delivered the major part of the prey items (67.9%), and the major part of the prey items delivered by the male was birds (80%) (Figure 1). The probability that a prey item

was delivered by the male was significantly higher for birds than for mammals (Figure 1, Table 2).
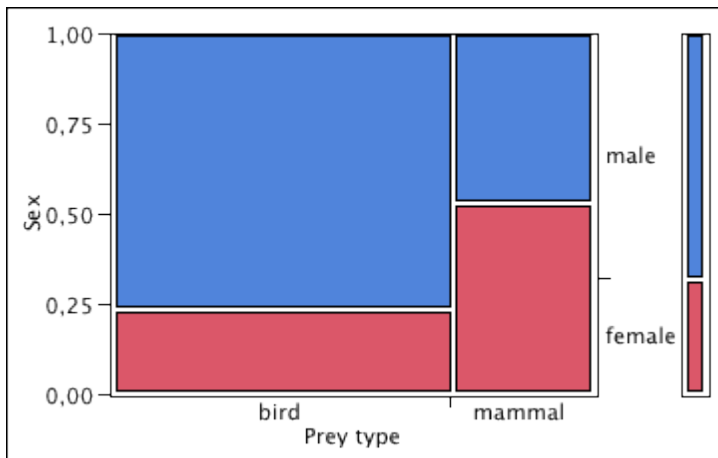

Figure 1. The distribution of prey type (bird or mammal) on delivering sex for the 162 prey items recorded delivered at the nest where the sex of the eagle delivering the item was determined.

There was a significant effect of prey type on the probability that a prey item was delivered at the nest by the male (Table 2). Prey body mass, age of the nestlings and relevant interactions did not have a significant effect on the probability that an item was delivered by the male.

Table 2. Results from a likelihood ratio test in a logistic regression model with sex as response variable and prey type (birds or mammals) as explanatory variable (N = 162).

Term	Estimate	SE	df	χ^2	p
Intercept	0.5268	0.1829			
Prey type	0.6546	0.1829	1	13.03	0.0003

Selection of willow grouse as prey

The probability that a prey item delivered at the nest was a willow grouse rather than any other prey was significantly affected by age of the nestlings, by the interaction between time since midday and whether the delivery was made before or after midday, and by the interaction between ambient temperature at the time of delivery and whether the delivery was made before or after midday (Table 3). The age of the nestlings reflects time of season (from late May to late July), so the decreasing probability that a prey delivered was a willow grouse

with increasing age means that the probability that a prey taken by the golden eagles was a willow grouse decreased throughout the season (Table 3).

Table 3. Logistic regression model of effects on the probability that a prey item delivered at the nest was a willow grouse. Whole model N = 159, χ^2 = 17.03, df = 6, p = 0.0092.

Explanatory variables	Estimates	SE	df	χ^2	p
Intercept	0.6425	1.1311			
Time since midday	-0.1182	0.0829	1	2.12	0.15
Before or after midday	-0.0353	0.1831	1	0.04	0.85
Temperature	0.0643	0.0786	1	0.67	0.41
Age	-0.0424	0.0171	1	6.49	0.011
Time since midday * Before or after midday	-0.1798	0.0800	1	5.37	0.020
Before or after midday * Temperature	-0.1784	0.0751	1	5.97	0.015

There was a tendency that a prey item delivered at the nest was less likely to be willow grouse later in the season when using age of the nestlings as a variable for season (Figure 2).
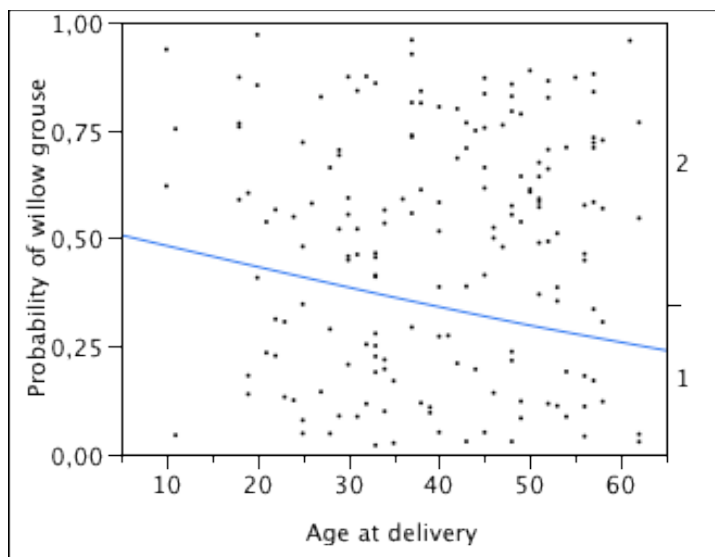
Figure 2. The probability that a prey delivered by the golden eagles was a willow grouse as a function of age of nestlings (1 = willow grouse, 2 = not willow grouse). Whole model N = 171, χ^2 = 2.47, df = 1, p = 0.12.

At the prey deliveries median air temperature was 11.5 °C. For temperatures lower than or equal to 11.5 °C, time since midday and age of the nestlings had a significant effect on the probability of a prey item delivered at the nest being a willow grouse (Table 4). The

probability of willow grouse being delivered at the nest decreased with time since midday and with nestling age, i.e. decreased throughout the season because age of the nestlings reflected time of season (Table 4).

Table 4. Logistic regression of effects on the probability that a prey delivered at the nest was a willow grouse when ambient temperature was less than or equal to the median of 11.5 °C for the period June-July 2011. Whole model N = 83, χ^2 = 7.78, df = 2, p = 0.020.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	1.9955	1.0741			
Time since midday	-0.2275	0.1079	1	4.84	0.028
Age	-0.0531	0.0236	1	5.65	0.018

When ambient temperature was less than or equal to 11.5 °C there was a tendency that more willow grouse were taken as prey around midday and decreasing probability with distance from midday (Figure 3). This opts for a higher relevance of the height of the sun rather than air temperature for the activity of the willow grouse, and thus a higher probability of predation around midday when the effect of sun rays peaks. The tendency in Figure 3 is non-significant because age of the nestlings (season) has not been accounted for.
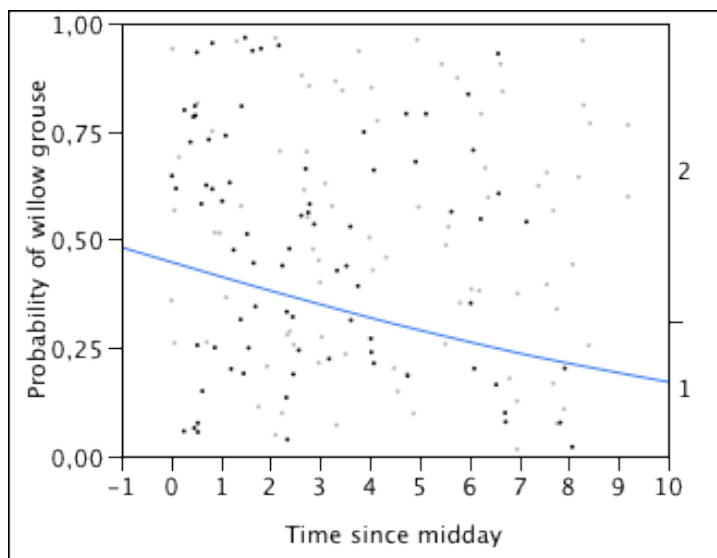

Figure 3. The probability that a prey delivered at the nest was a willow grouse as a function of time since midday when ambient temperature was less than or equal to 11.5 °C (1 = willow grouse, 2 = not willow grouse). Whole model N = 83, χ^2 = 2.14, df = 1, p = 0.14.

When ambient temperature was higher than the median of 11.5 °C for the period June-July 2011, only the interaction between time since midday and whether the prey was delivered before or after midday had a significant effect on the probability that a prey delivered at the nest was a willow grouse (Table 5). However, age of the nestlings was included in the model to control for time of season.

Table 5. Logistic regression of effects on the probability that a prey delivered at the nest was a willow grouse when ambient temperature was higher than the median of 11.5 °C for the period June-July 2011. Whole model N = 79, χ^2 = 7.98, df = 4, p = 0.092.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	0.9890	1.1126			
Time since midday	-0.0414	0.1304	1	0.10	0.75
Before or after midday	-0.2057	0.2701	1	0.60	0.44
Age	-0.0342	0.0224	1	2.37	0.12
Time since midday * Before or after midday	-0.2438	0.1280	1	4.083	0.043

Before midday and when ambient temperature was above 11.5 °C, there was a tendency to an increased probability of a prey item delivered at the nest being a willow grouse as time changed from morning to midday (Figure 4a). On the contrary, after midday there was a tendency to an increased probability of a prey being a willow grouse towards the evening when ambient temperature was above 11.5 °C (Figure 4b). Thus, when temperature was higher than 11.5 °C the probability of a prey delivered being a willow grouse increased from morning to evening.

a)   b)
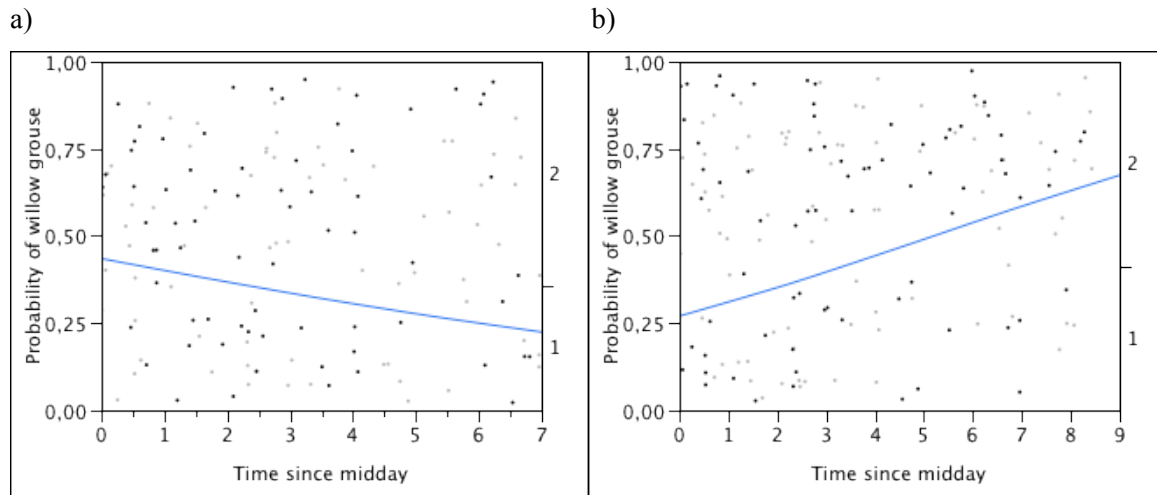
Figure 4. The probability that a prey item delivered at the nest was a willow grouse when ambient temperature was above 11.5 °C (1 = willow grouse, 2 = not willow grouse). a) Before midday: Whole model N = 31, χ^2 = 0.57, df = 1, p = 0.45. b) After midday: Whole model N = 51, χ^2 = 2.42, df = 1, p = 0.12.

Win-stay or win-shift hunting strategy

The probability that a prey item delivered at the nest (N) was the same species as the previous prey (N-1) decreased over season, with age of the nestlings reflecting season (Figure 5). Age of the nestlings was the only variable significantly affecting the probability that a prey species delivered at the nest was the same as the previous prey (N-1). Neither time since last prey delivery, change in date since last delivery or prey body mass significantly affected the probability that a prey item was the same as the previous item. Only prey items delivered by the male golden eagle were included in the model because the female potentially could have received a prey item from the male before delivery at the nest.
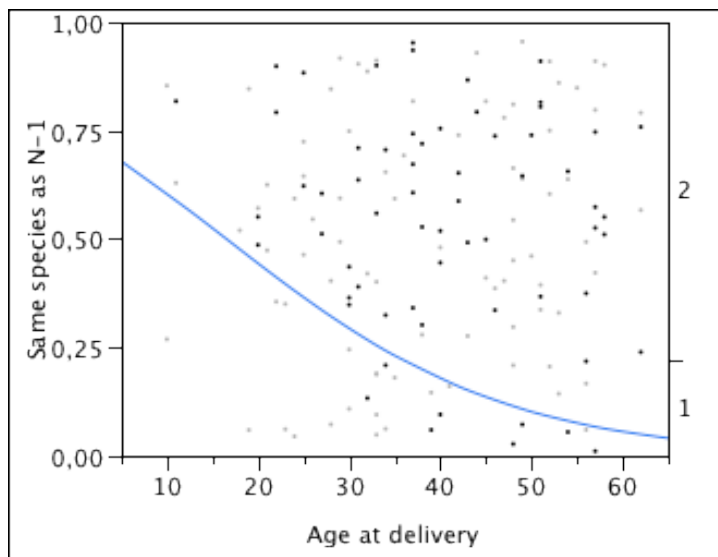
Figure 5. The probability that a prey item delivered by the male golden eagle at the nest was the same as the previous species (N-1) delivered as a function of season, with age of the nestlings reflecting season (1 = same species, 2 = not same species). Whole model N = 68, χ^2 = 8.44, df = 1, p = 0.0037.

The probability that the present prey item (N) delivered at the nest was a willow grouse when the previous prey delivered (N-1) was a willow grouse was significantly affected by time since last prey delivery only (Table 6). The probability increased with time since last prey delivery, measured in hours (Figure 6). Change in date and age of the nestlings did not significantly affect the probability. Only prey delivered by the male golden eagle were included in the model.

Table 6. Logistic regression of effects on the probability that the present prey item delivered at the nest was a willow grouse when the previous prey delivered was a willow grouse (N = 30).

Explanatory variables	Estimate	SE	χ^2	df	p
Intercept	1.1129	0.6268			
Time since last delivery	-0.1511	0.0804	4.71	1	0.030

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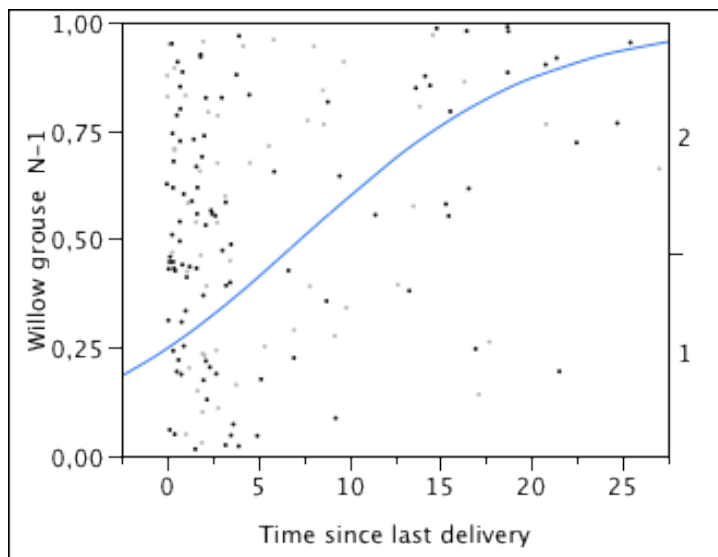
Figure 6. The probability that the present delivered prey and the previous delivered prey at the nest was a willow grouse as a function of time since last delivery, measured in hours (1 = willow grouse, 2 = not willow grouse). Only prey items delivered by the male were included. Whole model N = 30, χ^2 = 4.71, df = 1, p = 0.03.

The probability that the present delivered prey item (N) was a thrush when the previous prey (N-1) delivered at the nest was a thrush was significantly affected by time since last prey delivery and age of the nestlings (Table 7). The probability increased with age of the nestlings reflecting season (Table 7), but decreased with time since last delivery (Figure 7). Only prey items delivered by the male golden eagle were included.

Table 7. Logistic regression of effects on the probability that the present prey delivered was a thrush when the previous prey item delivered at the nest was a thrush. Whole model N = 18, χ^2 = 10.60, df = 2, p = 0.005.

Explanatory variables	Estimate	SE	χ^2	df	p
Intercept	-12.7336	8.2628			
Time since last delivery	0.7870	0.05018	8.54	1	0.0035
Age	0.2358	0.1553	7.53	1	0.0061
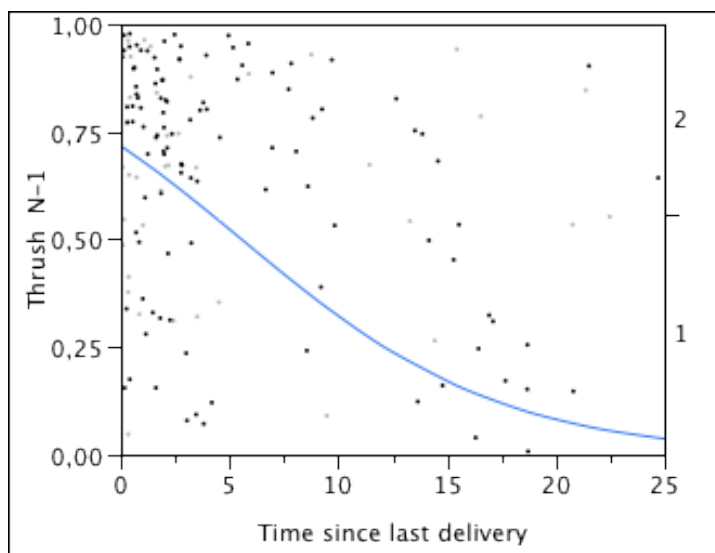
Figure 7. The probability that the present prey delivered was a thrush when the previous prey item delivered was a thrush as a function of time since last delivery, measured in hours (1 = thrush, 2 = not thrush). Only prey items delivered by the male golden eagle were included. Whole model N = 18, χ^2 = 3.077, df = 1, p = 0.079.

Prey handling before delivery at the nest

The probability that a prey was decapitated or partitioned before delivery at the nest was significantly higher for birds than for mammals, increased significantly with prey body mass and decreased significantly with nestling age (Table 8). There was also a significant interaction effect of prey type and prey body mass (Table 8). There was no significant effect of the interaction between prey type and age of the nestlings or between prey body mass and age of the nestlings.

Table 8. Logistic regression model of the probability that a prey item delivered at the nest was decapitated or partitioned. Whole model N = 163, χ^2 = 75.87, df = 4, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-0.9763	0.7070			
Prey type	1.2635	0.2950	1	26.30	< 0.0001
Body mass	0.0041	0.0007	1	53.87	< 0.0001
Age	-0.0371	0.0164	1	5.25	0.022
Prey type * Body mass	0.0021	0.0007	1	10.24	0.0014

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For birds the probability of being decapitated or partitioned increased significantly with prey body mass, and birds with an estimated body mass > 300 g had a probability of being decapitated or partitioned of > 50% (Figure 8a). Also for mammals, the probability of a prey item being decapitated or partitioned increased with prey body mass, and mammals with an estimated body mass > 1300 g had a probability of being decapitated or partitioned of > 50% (Figure 8b). There was a high probability of a prey being decapitated or partitioned even for smaller birds, while for mammals the probability increased less pronounced with body mass (Figure 8a, b). Thus, smaller mammals were more likely to be delivered whole than smaller birds.

a)   b)
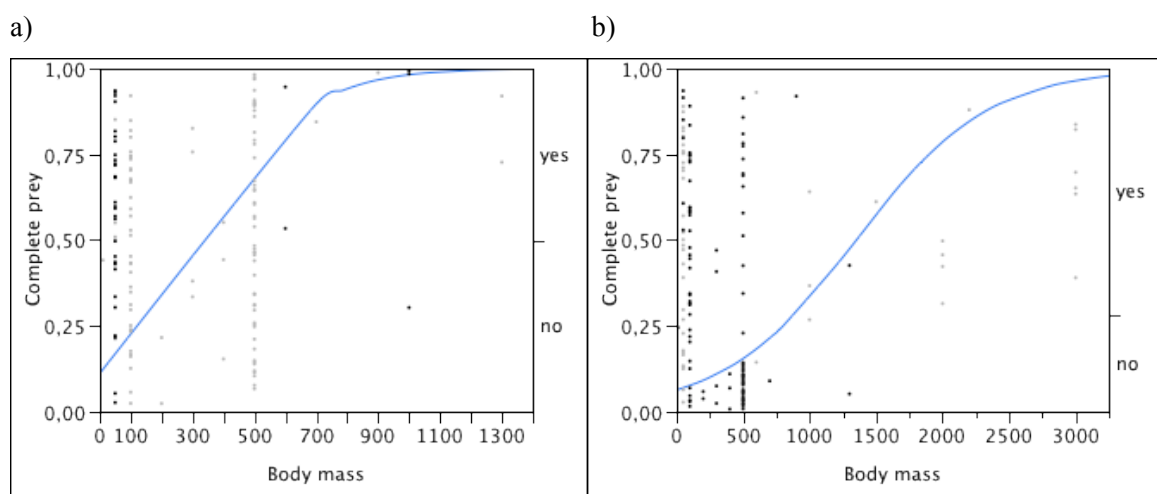
Figure 8. The probability that a prey item delivered at the nest was decapitated or partitioned before delivery as a function of prey body mass. a) Birds: Whole model N= 117, χ^2 = 37.22, df = 1, p < 0.0001. b) Mammals: Whole model N = 50, χ^2 = 28.74, df = 1, p < 0.0001.

The probability that a prey item was plucked before delivery at the nest was significantly affected by prey type (bird or mammal), prey body mass, and the interaction between prey type and prey body mass (Table 9). Birds were more often plucked than mammals, and the probability of being plucked increased with prey body mass, as well as for the interaction between prey type and prey body mass (Table 9). The delivering sex, age of the nestlings and relevant interactions had no significant effects on the probability of a prey item being plucked before delivery at the nest.

Table 9. Logistic regression model of the probability that a prey item was plucked before delivered at the nest. Whole model N = 162, χ^2 = 84.34, df = 3, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-1.5500	0.4103			
Prey type	2.1678	0.3505	1	77.40	< 0.0001
Body mass	0.0031	0.0007	1	26.37	< 0.0001
Prey type * Body mass	0.0019	0.0007	1	8.46	0.0036

Prey handling at the nest

The probability of plucking an item in the nest as preparation of the prey before feeding was significantly affected by the net body mass of the prey item and by whether the feeder was the female or the nestlings (Table 10). The probability that a prey item was plucked in the nest decreased with prey body mass, leaving smaller items less likely to be plucked before feeding. There was a higher probability that an item was plucked in the nest by the female than by the nestlings (Table 10). Prey type (bird or mammal), age of nestlings and interactions between the explanatory variables had no significant effect on the probability that a prey item was plucked in the nest.

Table 10. Logistic regression model of the probability that a prey item was plucked in the nest. Whole model N = 162, χ^2 = 14.24, df = 2, p = 0.0008.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	2.5626	0.3832			
Net body mass	-0.0011	0.0005	1	3.99	0.046
Feeder	-0.6460	0.3040	1	5.20	0.023

Of the 181 prey items delivered at the nest, handling was recorded for 166. The female and the nestlings handled 83 prey items each. The probability that the female fed the nestlings rather than the nestlings fed unassisted was significantly affected by prey type (bird or mammal), net body mass of the prey item, age of the nestlings, as well as the interaction between age of the nestlings and prey type (Table 11). There was a higher probability that the female fed the nestlings with avian than mammalian prey and the probability that the female fed increased with net body mass of the prey, but decreased with age of the nestlings. The

probability that the female fed the nestlings also increased with the interaction between age of the nestlings and prey type (Table 11).

Table 11. Logistic regression model of the probability that the female fed the nestlings rather than the nestlings fed unassisted. Whole model N = 166, χ^2 = 152.16, df = 4, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	14.1053	2.8145			
Prey type	1.5576	0.4961	1	13.42	0.0002
Net body mass	0.0095	0.0020	1	54.79	< 0.0001
Age	-0.4552	0.0914	1	99.86	< 0.0001
Age * Prey type	0.1999	0.0703	1	10.40	0.0013

For both avian and mammalian prey the probability that the female fed the nestlings rather than the nestlings fed unassisted decreased with age of the nestlings (Figure 9a, b). The probability that the female fed the nestlings decreased rapidly for avian prey when the nestlings reached c. 40 days of age, and nearly all avian prey was ingested by the nestlings unassisted when the nestlings was > 40 days old (Figure 9a). For mammalian prey the probability that the female fed the nestlings decreased less rapidly than for birds, but reached 50% a few days earlier than for birds (Figure 9b). The female fed the nestlings with mammalian prey until fledging (Figure 9b).

a)   b)
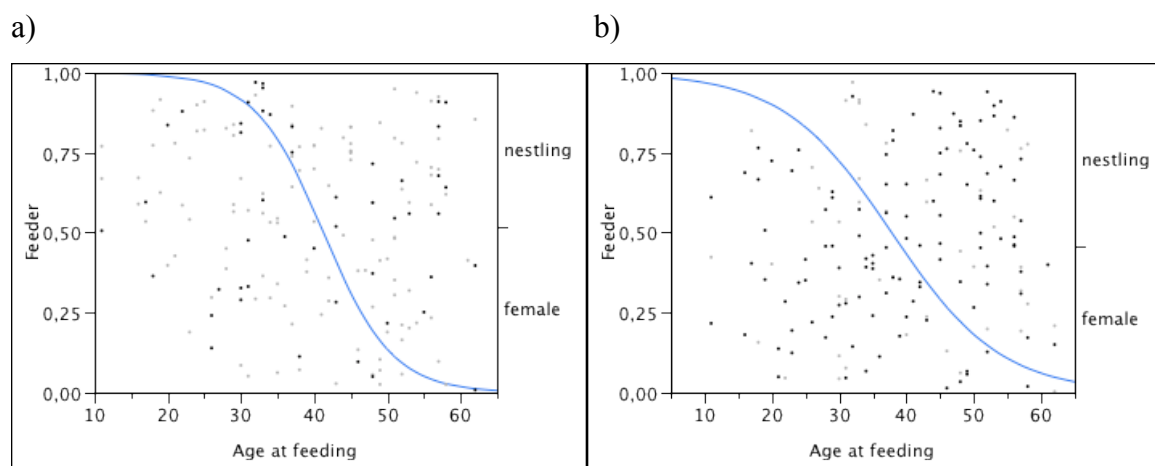

Figure 9. The probability that the female fed the nestlings rather than the nestling fed unassisted as a function of age of the nestlings. a) Birds: Whole model N = 118, χ^2 = 77.71, df = 1, p < 0.0001. b) Mammals: Whole model N = 48, χ^2 = 19.19, df = 1, p < 0.0001.

For prey items handled by the female number of meals per prey item was significantly affected by net body mass of prey, nestling age and the interaction between prey type (bird or mammal) and net body mass (Table 12). Number of meals per prey item increased with net body mass of prey and decreased with nestling age (Table 12). The increase in number of meals in interaction with net prey body mass was higher for mammalian than avian prey when the female handled prey.

Table 12. Generalized linear model (GLM) of significant effects on number of meals per prey when the female feeds the nestlings. Whole model N = 82, χ^2 = 61.27, df = 4, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	0.6523	0.1755			
Prey type	0.0414	0.0718	1	0.34	0.56
Net body mass	0.0011	0.0002	1	47.29	< 0.0001
Age	-0.0161	0.0048	1	11.13	0.0008
Prey type * Net body mass	0.0004	0.0001	1	7.75	0.0054

For prey items handled by the nestlings unassisted, only net body mass of prey and the interaction between prey type (bird or mammal) and net body mass of prey when delivered at the nest had a significant effect on the number of meals per prey (Table 13). Number of meals increased with net body mass of a prey item (Table 13). Age of the nestlings did not significantly affect number of meals of a prey item.

Table 13. Generalized linear model (GLM) of significant effects on number of meals per prey when the nestlings feed unassisted. Whole model N = 80, χ^2 = 85.93, df = 3, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-0.1025	0.0654			
Prey type	0.0522	0.0472	1	1.24	0.27
Net body mass	0.0014	0.0002	1	74.89	< 0.0001
Prey type * Net body mass	0.0004	0.0002	1	8.20	0.0042

For avian prey handled by the nestlings, number of meals increased markedly for items > 500 g. For mammalian prey, number of meals did not increase as markedly with net body mass as it did for birds (Figure 10). Both avian and mammalian prey items with an estimated net body mass < 200 g were largely consumed in one meal (Figure 10).
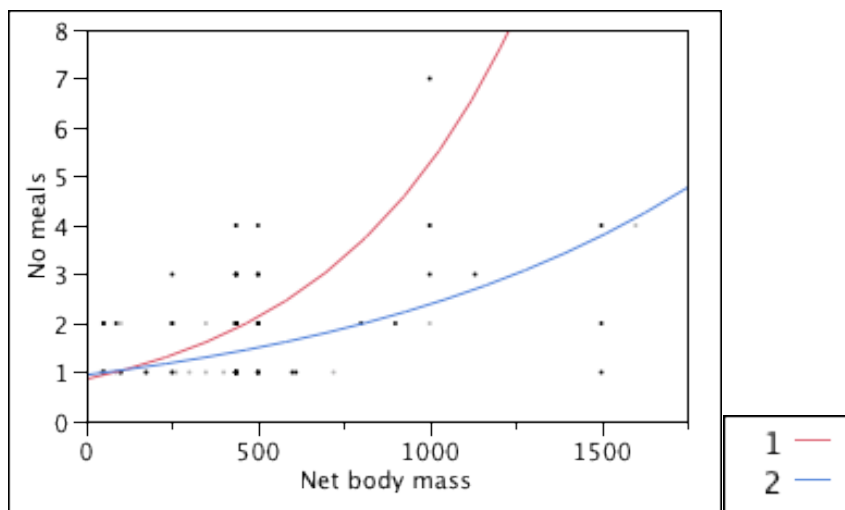
Figure 10. Number of meals as function of net body mass of prey, for birds (red line = 1) and for mammals (blue line = 2). Whole model N = 80, χ^2 = 85.93, df = 3, p < 0.0001.

For prey handled by the nestlings unassisted, the probability that a nestling monopolized a prey item was significantly affected by prey type (bird or mammal) and net body mass of the prey (Table 14). A prey item was monopolized when only one sibling fed of the prey and the prey was eaten in a single meal.

Table 14. Logistic regression model of the probability that a prey item was monopolized by one of the nestlings. Whole model N = 81, χ^2 = 47.65, df = 2, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-7.7024	2.1770			
Prey type	2.7467	1.1705	1	6.87	0.0087
Net body mass	0.0129	0.0033	1	47.09	< 0.0001

For both avian and mammalian prey, the probability that a nestling monopolizing a prey item decreased with increasing net body mass of the prey (Figure 11a, b), and smaller prey items had thus a higher probability of being monopolized. For avian prey the probability of monopolization was high for items < 100 g (Figure 11a), while for mammalian prey the nestlings monopolized prey items < 900 g (Figure 11b). Hence, mammalian prey was monopolized more often than avian prey.
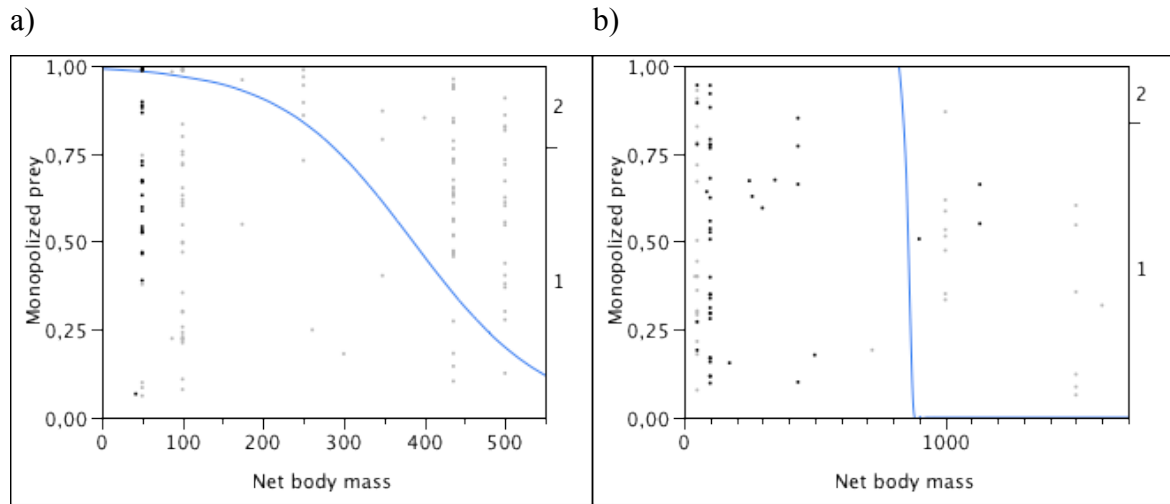
Figure 11. The probability that a prey item was monopolized by one of the nestlings as a function of net body mass of prey (1 = monopolized, 2 = not monopolized). a) Birds: Whole model N = 56, χ^2 = 26.20, df = 1, p < 0.0001. b) Mammals: Whole model N = 25, χ^2 = 21.98, df = 1, p < 0.0001.

For prey items handled by the female, handling time was significantly affected by net body mass of prey, age of nestlings, and prey type (bird or mammal) (Table 15). Handling time increased with increasing net body mass of prey, and decreased with age of the nestlings. Feeding category (1–4) was included in the model to correct for monitoring error.

Table 15. Generalized linear model (GLM) of significant effects on handling time of prey when the golden eagle female fed the nestlings. Whole model N = 82, χ^2 = 101.71, df = 6, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	7.3544	0.2234			
Prey type	0.1955	0.0937	1	4.60	0.032
Net body mass	0.0014	0.0002	1	70.99	< 0.0001
Age	-0.0267	0.0062	1	19.57	< 0.0001
Category feeding			3	19.66	0.0002

For prey items handled by the nestlings unassisted, handling time was significantly affected by net body mass of prey, prey type (bird or mammal), the interaction between prey type and net body mass of prey, and the interaction between prey type and age of nestlings (Table 16). Handling time increased with increasing net body mass of prey and was higher for mammalian than for avian prey with increasing body mass of the prey (Table 16).

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Table 16. Generalized linear model (GLM) of significant effects on handling time of prey when nestlings feed unassisted. Whole model N = 80, χ^2 = 339.59, df = 8, p < 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	3.3910	0.8956			
Prey type	0.3374	0.1631	1	5.22	0.022
Net body mass	0.0040	0.0003	1	169.85	< 0.0001
Age	0.0268	0.0165	1	2.88	0.090
Category feeding			3	30.46	< 0.0001
Prey type * Net body mass	0.0019	0.0003	1	37.18	< 0.0001
Prey type * Age	-0.0578	0.0173	1	13.41	0.0002

Discussion

Prey delivery

Prey delivered at the nest

Of the 181 prey items recorded delivered at the nest by the golden eagles during the nestling period, 70% of the items were birds and 30% mammals. Approximately one third of the prey items were willow grouse, whereas thrushes and small rodents made up 24 and 20% by numbers, respectively. Mountain hare comprised 7% of the diet by numbers. Birds as the most dominant prey type correspond to findings in other studies of the diet of golden eagles in northern Europe (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007). Species of grouse and lagomorphs are considered main prey of the golden eagles (Valkama et al. 2005; Watson 2010), and the relatively large amount of willow grouse in the golden eagle diet in my study was thus expected. However, the composition of the diet varies considerably between regions and over years, reflecting differences in prey availability (Watson 2010). Watson et al (1993) performed line transects counts of numbers of grouse and lagomorphs in seven regions in Scotland, and the proportion of grouse and lagomorphs found in the diet of golden eagles highly reflected the relative number obtained from the line transect counts.

In the area of Møsvatn, near my study area, population estimates of willow grouse have been obtained every year since 1992, and have revealed a decline in population size (Framstad 2011). Line transect counts from 2010 gave some of the lowest estimates of willow grouse densities in the period 1992–2010 (4 ptarmigan/km^2) (Framstad 2011), and one would thus expect other prey types than willow grouse to be the most common prey item delivered at the golden eagle nest in 2011. Nonetheless, willow grouse was the most important prey, both by number and by mass (34% and 35%, respectively). Tjernberg (1981) and Watson et al (1993) observed grouse making up 54.3% and 47.8% by number, respectively, of the diet of golden eagles during the summer, indicating that this prey type may make up a higher proportion in years of good accessibility. However, the high proportion of grouse found in these diet analyses might as well be a result of traditional methods applied, where larger birds tend to be overestimated as prey. When preferred prey are scarce golden eagles would seek alternative prey, and the overall breadth of the diet would increase (Watson 2010). This might explain the relatively high number of thrushes in the diet. Voles and lemmings were also important in the diet by numbers, which is in accordance with the high capture of small rodents at Møsvatn

in 2010 and 2011, indicating a dense population (Framstad 2011). The fact that the golden eagles included small prey items to such a large extent in the diet could be explained by a higher ingestion rate for small than for large prey, making them important as prey in the breeding diet (Slagsvold & Sonerud 2007).

There were no recorded ungulates in the diet of the monitored eagles. This was somewhat unexpected, since several previous studies of the diet of golden eagles in northwest Europe have recorded as much as 10% of the diet consisting of reindeer (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007). Both reindeer and sheep were available as prey in immediate vicinity to the nest (pers. obs.). Some studies have further pointed at the golden eagle as an important predator on reindeer calves during the breeding season (Nybakk et al. 1999; Norberg et al. 2006). There are other large predators in the area of the monitored eagles, mainly lynx (*Lynx lynx*) and wolverine (*Gulo gulo*), presumably posing a bigger threat on reindeer calves and lambs. Golden eagles are known to scavenge carrion frequently, especially during winter months (Watson 2010), and to what extent the golden eagle hunt and kill ungulates themselves or scavenge what other predators has killed, or if the prey has died from other causes, remains controversial.

This is the first study, to my knowledge, where the diet of golden eagles has been assessed by video monitoring at the nest. The use of direct observation methods by video monitoring might explain why I found a higher proportion of smaller prey items and smaller proportion of larger prey, such as grouse and hare, in the diet of the golden eagles I studied than in other previous studies. The traditional indirect methods of collecting regurgitated pellets or prey remains at the nest at the end of a breeding season, has proved to be subject to various biases concerning both the number of prey delivered and the proportion of different prey items in the diet (Tjernberg 1981; Collopy 1983; Simmons et al. 1991; Lewis et al. 2004; Selås et al. 2007; Tornberg & Reif 2007; Homme 2008; Slagsvold et al. 2010; Watson 2010). This can lead to misinterpretation of the importance of different groups of prey in the diet, with typical overestimation of larger prey items and underestimation of smaller items when analysing prey remains (Simmons et al. 1991; Redpath et al. 2001; Lewis et al. 2004; Selås et al. 2007; Tornberg & Reif 2007). Analysis of pellets, on the other hand, tend to overestimate smaller prey items in the diet, especially smaller mammals (Lewis et al. 2004). Prey remains and pellets also suffer from various degrees of degradation for different prey types (Lewis et al. 2004), making some groups of prey either more conspicuous or undetectable (Tjernberg

1981). This could explain why several studies where the diet of the golden eagle has been assessed, has found ungulates such as reindeer to compose a rather large proportion of the diet (Nyström et al. 2006; Johnsen et al. 2007). Also, smaller prey items, such as voles and passerines, were most often observed swallowed whole by the golden eagle nestlings, leaving no remains, only pellets (pers. obs.). This has also been observed in several other studies of raptors using video recording (Steen 2004; Tornberg & Reif 2007; Slagsvold et al. 2010). The regular removal of remains from the nest by the female was observed as well, as is known to occur in some breeding pairs of golden eagles (Tjernberg 1981). Video monitoring provides a more accurate description of the diet of raptors during the nestling period, and also allows a larger sample size (Lewis et al. 2004; Homme 2008).

The delivering sex

The male delivered 68% of all the prey items recorded delivered at the golden eagle nest. Distinct parental roles during the breeding season is well documented amongst nearly all species of raptors, with the male doing most of the hunting and providing of food for the female and the nestlings, and the female most of the incubation and parental care at the nest (Newton 1979). In my study, the male provided food for the female and the nestlings, while the female exclusively brooded and fed the nestlings, as described in Watson (2010). Of the prey items delivered by the male 80% were birds, whereas the total percentage of birds in the diet was 70%. A large proportion of birds in the diet of raptors has previously been linked to a high degree of reversed sexual size dimorphism (RSD), i.e. the female being larger than the male (1979). The golden eagle is highly dimorphic with the female eagle weighing as much as 40-50% more than the male and having up to 10% greater wing-lengths than males (Watson 2010). Slagsvold & Sonerud (2007) has pointed towards the fact that raptors rely on preparation of large prey for their size, spending more time in the nest feeding the nestlings small morsels of prey and thus further dividing parental roles between the male and the female for efficient food provisioning and ingestion. Slagsvold & Sonerud (2007) also propose an alternative hypothesis of RSD much similar to that of Newton (1979), namely that males are smaller than females so they can catch smaller, agile prey such as birds during breeding. This might explain why the male eagle provides such a high amount of birds to the nest as observed. Further, the larger body size of the female is linked to brooding and defence of off-spring during the nestling period, but also for catching larger prey outside the breeding season when preferred prey is scarce, as well as for reducing the risk of a negative energy

budget in periods with low temperatures. Hence, female survival during winter months might in this way be higher than male survival (Slagsvold & Sonerud 2007).

Selection of willow grouse as prey

The probability that a prey item delivered at the golden eagle nest was a willow grouse rather than any other prey item decreased throughout the season. This could be explained by a higher availability of other prey towards the end of the breeding season, such as passerine fledglings and voles and lemmings. Another explanation could be that the willow grouse is more vulnerable to predation in the early stages of the breeding period (Sonerud 1985; Hannon et al. 2003). Hannon et al (2003) found that female willow grouse ran a higher risk of predation in the late pre-laying period, during incubation and in the pre-fledging brood rearing period. After fledging the willow grouse chicks are no longer immobile and can actively escape a predator, and the female also deduce her distraction display (Sonerud 1985; Hannon et al. 2003). Hence, the willow grouse has potentially a reduced risk of predation later in the season, and fewer willow grouse are thus taken as prey by the golden eagles.

When season was accounted for the probability of a prey item delivered being a willow grouse peaked around midday on cold days and in the evening on warm days. This pattern may be due to the activity of the willow grouse. On cold days there might be a higher relevance of the height of the sun rather than ambient temperature for when the willow grouse female recess from incubation to forage. Grouse have to forage fast during incubation recess to reduce time spent away from the eggs, and might be less vigilant and thus more vulnerable to predation. Later, when the willow grouse chicks hatch, they start foraging for insects, which rapidly increases vulnerability. It is likely that the activity, and hence availability of insects increase around midday when cold, and willow grouse would thus concentrate foraging for insects around midday. Hence, willow grouse would be more exposed to predation at this time. On warm days, however, the activity of insects are probably higher around evening, and the activity of the willow grouse is thus also likely to increase at this time of day, again increasing vulnerability and risk of predation.

Win-shift and win-stay hunting strategy

In my study, the probability that the male golden eagle delivered a prey item of the same species as the previous item decreased throughout the season. A possible explanation for this could be, as for the probability of delivering a willow grouse that the availability and diversity of prey increases from early to late in the season. However, for the two most important groups of prey by number, willow grouse and thrushes, this turns out quite differently. The probability of delivering a willow grouse when the previous prey also was a willow grouse was only affected by time since last delivery of a willow grouse, and not by season, while the probability of delivering a thrush when the previous prey also was a thrush was affected both by time since last delivery of a thrush and by season. The probability increased with increasing time since last delivery for willow grouse, while the opposite was true for thrushes where the probability also increased from early to late in the season.

The higher probability of delivering a willow grouse with increasing time since last delivery of a willow grouse could be explained by the relatively large body mass of this prey type, and thus a lack of need for rapid delivery of this particular prey. However, I find a more likely explanation to be the choice of hunting strategy of the eagles. For a single-prey loaded central place forager, like the golden eagle during breeding season, Sonerud (1985) outlined three options for a predator facing a new hunt after a prey delivery at the central place depending on distribution of prey. For randomly distributed prey the predator should search at random, for uniformly distributed prey scattered after an initial capture the predator should wait before returning to the capture site, while for clumped prey the predator should rapidly return to the capture site increasing its chance of success rather than searching at random (Sonerud 1985). These strategies are based on the theory that a predator remembers a capture site with high precision after a visit, indicating a well developed topographic memory (Sonerud 1985; Mitchell & Lima 2002). Hence, a predator´s choice of where to search for prey will be based on the memory of previous capture or detection sites (Sonerud 1985; Mitchell & Lima 2002). Willow grouse will potentially be more vigilant and scatter out after an initial attack from a predator, and might also move away when the predator is out of sight to reduce the risk of predation (Sonerud 1985; Mitchell & Lima 2002). The level of vigilance of the willow grouse will decrease as the risk of another encounter with a predator decreases (Mitchell & Lima 2002; Roth & Lima 2007). The golden eagle should thus wait before returning to the encounter site in turn to increase unpredictability and hence its probability to capture willow

grouse (Roth & Lima 2007). This is termed a win-shift hunting strategy. The spatial and temporal unpredictability of a predator hunting prey has been investigated by Roth & Lima (2007), who observed a win-shift strategy in radio-tagged sharp-shinned hawks (*Accipiter striatus*) hunting avian prey. Prey were highly vigilant after an attack and the hawks thus benefitted from extending their time of return to the capture site and instead visit another site (Roth & Lima 2007).

In contrast, thrushes were more likely to be delivered in "runs", with decreasing probability as time since last delivery increased. The most common of the thrushes, the fieldfare, often breed in colonies (Svensson et al. 2004) and therefore have a clumped distribution as prey. Hence, the eagle probably remembered its successful encounters with the thrushes, and adjusted its decision to return to the capture site where the probability of another successful hunt was high (Sonerud 1985; Mitchell & Lima 2002). The use of a win-stay strategy by the golden eagles when hunting thrushes is likely, and the eagles were even observed to deliver whole thrush nests on several occasions (pers. obs.). Studies on the Eurasian kestrel has also indirectly documented the use of a win-stay strategy (Steen 2004; Løw 2006), which is believed to be common in single-prey loaded central place foraging birds (Sonerud 1985). The increasing probability throughout the season of delivering a thrush when the previous prey was a thrush could be a response to increased availability of thrush fledglings. Newly fledged thrushes are sometimes helplessly moving around on the ground, making them an easy target for predators.

Prey handling before delivery at the nest

There was a higher probability of birds than of mammals being decapitated or partitioned prior to delivery at the nest. Similarly, Steen (2004) and Løw (2006), studying the Eurasian kestrel, found that more birds than mammals were decapitated before delivery at the nest. The head of a bird or a mammal may be too large or risky for a nestling to swallow. Following a swallowing threshold model presented by Kaspari (1990), prey items too large to swallow whole should be prepared before feeding. Time spent preparing a prey item should also increase with increasing size of the prey (Kaspari 1990) and the parts of a prey item contributing most to its width should be removed, following a width reduction hypothesis

(Kaspari 1991). The feeding constraint hypothesis (Slagsvold & Wiebe 2007), addressed by Steen et al (2010), states that the gape size limit prevents young nestlings of swallowing skulls. Further, gape size limit and swallowing capacity are age dependent, and the probability of decapitation decreased with nestling age and increased with prey size for the Eurasian kestrel (Steen et al. 2010). My findings, that the probability of decapitation or partitioning increased with the size of the prey and decreased with nestling age, is consistent with the feeding constraint hypothesis. For avian prey the probability of decapitation or partitioning prior to delivery increased markedly with the increase in body mass of the prey item, with > 50% probability for birds > 300 g, while for mammals there was > 50% probability for prey items > 1300 g being decapitated or partitioned before delivery at the nest. Smaller mammals are probably less difficult to swallow whole than birds, which may explain why smaller birds were more likely to be prepared prior to delivery than smaller mammals. In terms of preparing a prey before delivery at the nest a single-prey central place forager may also decrease the load carried to the nest by removing parts less favourable to the nestlings like the head of a prey and feathers (Sodhi 1992). The distance between the capture site and the central place may as well alter the raptor´s decision to prepare a prey item, with increasing probability of preparing a prey item with increasing distance to the nest (Sodhi 1992). Løw (2006) suggested that the Eurasian kestrel prepared large avian prey more often by decapitation and plucking to reduce transport costs, and Aasen (2004) also suggested this after observing the same pattern in nesting sparrowhawks (*Accipiter nisus*). My observations that birds were more often plucked before delivery at the nest than mammals, and that the probability of plucking increased with prey mass is consistent with these findings.

Prey handling at the nest

The probability of plucking a prey item in the nest as further preparation before feeding increased with net body mass of the prey, and smaller items were thus less likely to be plucked in the nest. There was also a higher probability that the female plucked prey items in the nest rather than the nestlings. The nestlings more often monopolized smaller prey items, which were easier to swallow whole and needed less preparation before being ingested. Similar, monopolization of small prey items by nestlings was found in kestrels (Steen 2004) and Tengmalm´s owl (*Aegolius funereus*) (Kristiansen 2003). The eagle nestlings also

monopolized small mammalian prey more often than small avian prey, indicating that small mammals were easier to handle and swallow whole due to a more cylindrical form than avian prey. Only 14% of the items were in fact observed plucked in the nest, which may indicate that preparation of a prey item before delivery at the nest was of more importance than preparation in the nest. The golden eagle is a large raptor and it is likely that the swallowing capacity is high also for nestlings and that ingestion is well developed. The nestlings were observed to swallow feathers and fur from prey (pers. obs.), and plucking of prey items in the nest may not increase the efficiency in feeding very much.

The probability that the female handled a prey item and fed the nestlings rather than the nestlings handled unassisted was higher when the prey item was a bird and the probability increased with the body mass of the prey item, but decreased with the age of the nestlings. Birds would be more difficult to handle than mammals, with protruding parts like bill, feathers and long tarsi, and also a more complex skeletal structure. Time spent feeding from avian prey would thus be prolonged, and for various raptors feeding time has been shown to be longer for avian than for mammalian prey (Slagsvold & Sonerud 2007). The female eagle should therefore feed the young nestlings with avian prey, particular large avian prey such as grouse, and leave smaller mammals to the nestlings for self-feeding, as observed. As nestlings grow older their bill develops and they become more proficient at standing, and tearing up prey unassisted becomes easier (Watson 2010). At c. one month of age, the smaller nestling handled its first prey unassisted, in accordance with studies by Watson (2010), where the golden eagle nestling was c. 5 weeks old when its physical development was sufficient for self-feeding. Further, when the nestlings reached an age of > 40 days, almost all avian prey were handled by the nestlings unassisted, but the female continued to feed the nestlings mammalian prey until fledging at c. 62 days of age. The reason why the female fed the nestlings this late in the nestling period could be a function of prey size. The golden eagles delivered relatively large mammals like mountain hare and red fox, and larger prey items were more likely fed by the female. Another explanation could be that the female fed large prey to the nestlings even though they were capable of self-feeding to ensure that not just the dominant sibling monopolizes prey and obtain all food (Slagsvold 1997). Aasen (2004) observed that female sparrowhawks continued to feed nestlings after they were able to self-feed, and proposed that the female tried to ensure an even distribution of food between the nestlings. The latter explanation is probably of less importance in my study where both the dominant and the subdominant sibling monopolized a similar number of prey items (34 and

29, respectively), but still the total amount of energy gained from each prey item may have differed between the siblings.

When the female eagle fed the nestlings number of meals per prey item increased with prey body mass. Larger prey items were also more often fed in more than one bout in the Tengmalm´s owl (Kristiansen 2003). Feeding in more than one bout could be due to satiation after one meal, leaving the raptor to wait until gut space is large enough to fill up again (Slagsvold & Sonerud 2007; Slagsvold et al. 2010). Whether the prey item was a bird or a mammal did not affect the number of meals per prey, thus the size of a prey item was of more importance than prey type alone for an extended number of meals when the golden eagle female fed the nestlings. However, number of meals increased more for mammalian than for avian prey when net body mass of prey increased. This is in accordance with findings of Slagsvold et al (2010) where wild raptors of several species, including the golden eagle, kept in temporary captivity ingested a higher proportion of a mammalian prey than of an avian prey item. The proportion of an item ingested also increased with increasing body mass of the raptor (Slagsvold et al. 2010), which could opt for an extended number of meals as body mass of mammalian prey increases. Number of meals per prey item decreased with nestling age suggesting that as nestlings grew older and became able to self-feed, less assistance by the female was needed when feeding, and also bite size would increase and thus feeding efficiency would increase.

Also, when the nestlings fed unassisted number of meals per prey item increased with net body mass of the prey. However, number of meals did not decrease with nestling age. As the nestlings develop physically and becomes more capable of handling larger prey unassisted, more prey will be handled piece by piece instead of being swallowed whole (Kristiansen 2003). Hence, the nestlings handle larger prey items unassisted and number of meals thus increases. For both avian and mammalian prey items the number of meals increased with increasing net body mass of the prey, but more pronounced for avian than for mammalian prey. Avian prey with an estimated net body mass of more than 500 g had an almost exponential increase in number of meals, indicating that large avian prey were more difficult to handle by the nestlings than large mammalian prey (Slagsvold & Sonerud 2007). However, both avian and mammalian prey less than 200 g were largely consumed in a single meal.

The number of meals per prey item also reflects time spent handling a prey, and when the golden eagle female fed dependent nestlings the handling time increased with increasing net body mass of the prey item. This is in accordance with results from other studies on handling time in raptors (Kristiansen 2003; Aasen 2004; Steen 2004; Slagsvold & Sonerud 2007). Increased handling time with increasing body mass of prey is suggested caused by larger bones and stronger ligaments, as well as thicker skin and skull of larger prey (Slagsvold & Sonerud 2007). However, handling time was considerably longer for mammalian than for avian prey, which is in contradiction with most other studies on handling of prey by raptors (Kristiansen 2003; Aasen 2004; Steen 2004; Slagsvold & Sonerud 2007). The golden eagle is considered a bird feeder due to a large proportion of birds in the diet (Slagsvold et al. 2010), and bird feeders are considered more efficient than vole feeders when handling larger prey items and in particular larger avian prey (Slagsvold & Sonerud 2007). This could be as a result of evolving a long and narrow bill more specialized to pluck and tear up a prey, thus coping better with larger avian prey than vole feeders which swallow small prey items whole (Slagsvold & Sonerud 2007; Slagsvold et al. 2010). Mammalian prey delivered at a golden eagle nest may be quite large, and also considerably larger than avian prey delivered at the nest, and would thus take longer time to handle. When the female fed the nestlings, the handling time decreased with nestling age, suggesting an increase in gape size limit of the nestlings allowing the female to feed the nestlings with larger pieces, and thus decrease handling time. The observation of a shift in size of the pieces fed by the female from small to quite coarse pieces of meat as the nestlings grew older supports this (pers. obs.). This was also found for nesting sparrowhawks (Aasen 2004).

Also, for prey items handled by the eagle nestlings unassisted handling time of prey increased with increasing net body mass of the prey, as was the case for Eurasian kestrel nestlings studied by Steen (2004) and sparrowhawk nestlings studied by Aasen (2004). Age of the nestlings did not affect handling time, which could be caused by a similar handling time of small prey items more likely to be swallowed whole even when the nestlings were young, and a similar handling time of larger prey items after the nestlings became old enough to handle prey unassisted. Both small mammals and small birds were observed swallowed whole by the golden eagle nestlings. Handling time was higher for mammalian than avian prey also when the nestlings handled prey unassisted. The golden eagles delivered large mammalian prey at the nest, which considerably increased time spent handling the item compared to handling time of the smaller avian prey.

Implications and further prospects

The golden eagle is a widely distributed generalist raptor (Watson 2010), and local adaptations and specialization on specific prey types as a response to prey availability is thus likely to occur and will affect the composition of the diet. In this study I was able to video monitor at only one nest. Hence, the results may reflect the breeding diet of a golden eagle pair locally adapted and also reflect individual preferences. However, the results I obtained were similar to those from studies of the breeding season diet of the golden eagle both in Fennoscandia and Scotland (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007; Watson 2010). Still there are some differences regarding the lack of ungulates and the fairly large amount of small prey items in the diet of the video monitored golden eagles. This may be a result of previous indirect methods using prey remains or regurgitated pellets to estimate the diet, where larger prey items tend to be overestimated and small underestimated. The lack of ungulates in the diet could also be a result of starting video recording when the nestlings were c. 10 days old and not at hatching, where deliveries of ungulates could have been missed. However, when examining the nest bed when the nestlings were c. 15 days old no remains after such prey were observed (pers. obs.).

The use of the direct method of video monitoring a golden eagle nest in the wild has to the best of my knowledge never been done before. Video monitoring has become more common the past decade, and acknowledged as the method providing the most direct results regarding diet composition of breeding raptors. However, there might exist biases by using video recording as well. When the collection of prey remains and video monitoring were compared as methods to assess the diet of breeding goshawks (*Accipiter gentilis*), both number of prey items and number of prey species were underestimated by using video monitoring (Sveen 2006). This was probably due to the fact that only four days per nest and not the entire nestling period was video monitored, and not even complete days were covered (Sveen 2006). Identification of prey species from video monitoring may also lead to biases due to the view determined by the angle of the lens and frame-rate and picture quality of the recordings. However, technology is moving forward and improvement in the quality of video recordings is just a matter of time and resources. Either way, video recording is a time consuming method and can also suffer from various technical errors. Several studies on raptor diet during the breeding season hence suggest a combination of direct and indirect methods to reduce potential biases and time spent monitoring (Lewis et al. 2004; Sveen 2006; Homme 2008).

Regardless of biases that might occur when using direct observational methods, this is still the method providing the most reliable estimate of a raptor´s diet during breeding. The method also provides additional detailed data concerning delivery and handling of prey and general behaviour at the nest, which is difficult to obtain in other ways. The cost of prey handling may influence the selection of prey, and thus the importance of a prey type in the diet of a raptor. The unexpected amount of small prey items in the diet of the golden eagles is hence of interest, as well as the large proportion of willow grouse despite a low population size of this species in the area. This indicates a preference for willow grouse as prey, and could hence have implications for the management of this prey species. The willow grouse is a popular game species and hunting, both legal and illegal, impose additional stress on a population, which in this case is at a low density. This may have negative effects on population dynamics (Valkama et al. 2005). Management strategies of the willow grouse population in this area should thus be implemented, and restrictions on hunting ptarmigan species will be favourable since hunting mortality is additive to natural mortality (Smith & Willebrand 1999; Pedersen et al. 2004). Diet studies of raptors is thus important also for management of their main prey species, and hence for management of the raptor species in concern.

There is a need for continued video monitoring of breeding golden eagles to enlarge the so far small sample size of this method, and to include samples from various parts of the golden eagle range. Assessing handling efficiency through direct observational methods can reveal the relative profitability of different prey species in the diet of golden eagles during the breeding season. Handling efficiency is still to be assessed in golden eagles and is essential in understanding prey selection and feeding behaviour.

Conclusion

The most important prey type in the diet of the golden eagle pair was birds, and willow grouse was the dominating prey species both by number and by mass despite a small population of this prey species in the region. Small mammals and birds, such as voles and thrushes, were also important prey by numbers. No ungulates were observed delivered at the nest. This could opt for willow grouse as a preferred prey species, and also a higher importance of small prey than reported in the literature. The male golden eagle delivered the largest amount of prey to the nest. He also mainly delivered birds, and a higher proportion of birds than among prey delivered by the female. This supports the hypothesis of RSD in raptors, where the male is smaller than the female so that he can catch more agile prey during the nestling period. The use of a direct video-based observation method provided detailed information of the diet of the eagles during the breeding season, and thus the relative importance of different prey types in the diet. Video monitoring also provided valuable information on delivery and handling of prey. There is still a need for assessing handling efficiency of different prey to explain prey selection, and to also monitor the golden eagle breeding diet throughout its range. Management of the important prey species willow grouse is recommended in the region of the studied eagles.

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