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Diet and Prey Handling at a Nest of the Golden Eagle (*Aquila chrysaetos*) in Oppland County, Norway

Diett og byttedyrhåndtering på et reir av kongeørn (*Aquila chrysaetos*) i Oppland fylke, Norge

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Acknowledgements

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Abstract

The diet and prey handling of a breeding pair of the golden eagle (*Aquila chrysaetos*) in Oppland County, Norway, was analysed with video monitoring of prey deliveries at the nest during the ten weeks that the nestling stayed in the nest. The study was conducted in a year with regional low abundance of microtine rodents and willow grouse (*Lagopus lagopus*). A total of 71 prey items was recorded delivered at the nest, 43 items of these were identified to species level and 26 to genus. One prey was only identified as a bird, and one prey was not identified at all. The most common prey were birds (68%). In terms of number of prey delivered, thrush (*Turdus sp*.) (41%), mountain hare (*Lepus timidus*) (27%), and willow grouse (20%) were the most numerous species. Mountain hare was the most important prey (67%), while thrush and willow grouse made 7% and 20% of total delivered biomass, respectively. Only one microtine rodent was delivered at the nest. No deliveries of sheep (*Ovis aries*), parts of a sheep, or other livestock was recorded at the nest. The male delivered most prey items (57%), of which the largest proportion was birds (69%). The nestling started to feed unassisted at an age of 41 days, and fed unassisted on birds earlier than on mammalian prey, in contrast to what found in previous studies. Deliveries of mountain hare and willow grouse declined throughout the season, while deliveries of thrushes increased. My study suggests that the golden eagle's strategy when hunting willow grouse is win-shift, while the strategy on thrushes is win-stay. My study, as other studies based on video monitoring, has revealed a larger proportion of small prey species in the diet of the golden eagle, which is in contrast to studies based exclusively on prey remains and pellets. The high proportion of thrushes recorded indicates their importance in the golden eagles diet, especially in years with low abundance of other prey species. In consistence with other studies on the diet of golden eagle, mountain hare and willow grouse were the most important prey species in terms of biomass delivered.

Sammendrag

Diett og byttedyrseleksjonen til et par hekkende kongeørn (*Aquila chrysaetos*) i Oppland, Norge, ble analysert ved videoovervåkning av byttedyrleveringer, gjennom de ti ukene ungen var på reiret. Studien ble gjort i et år med regional lav tetthet av microtine smågnagere og lirype (*Lagopus lagopus*). Til sammen ble 71 byttedyr filmet levert på reiret, hvorav 43 byttedyr ble identifisert ned til art, og 26 til slekt. Et bytte ble bare bestemt som fugl, mens et byttedyr ikke ble identifisert. Det mest vanlige byttedyret var fugler (68%). I antall byttedyr levert til reiret var trost *(Turdus sp.)* (41%), hare (*Lepus timidus*) (27%) og rype (20%) de mest tallrike artene. Hare var det viktigste byttedyret (67%), mens trost og rype utgjorde henholdsvis 7% og 20% av den leverte biomassen. Bare en smågnagere ble levert til reiret. Det ble ikke registrert sau (*Ovis aries*), spor av sau eller andre husdyr levert på reiret. Hannen overleverte flest byttedyr (57%), hvorav fugler (69%) utgjorde den største andelen. Ungen spiste selvstendig først etter 41 dager, å spiste fugler selvstendig tidligere enn pattedyr, dette i motsetning til hva som er funnet i tidligere studier. Overleveringer av hare og rype avtok utover i sesongen, mens leveringer av trost økte. Min studie foreslår at kongeørn jakter med en win-shift strategi på lirype, og en win-stay strategi på trostefugl. Min studie som andre studier basert på kameraovervåkning, har avslørte en større andel små byttedyr i dietten til kongeørn, noe som er i uoverensstemmelse med studier basert på kun pellets og byttedyrrester. Den høye andelen trost i dietten indikerer også denne artens viktighet som byttedyr for kongeørn, særlig i år med lave tettheter av andre viktige byttedyr. I overenstemmelse med andre studier på kongeørndiett ble hare, og rype de viktigste byttedyrene i form av biomasse levert.

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Introduction

The breeding density and reproductive success of raptors' are limited by the abundance of their prey species because the amount of prey delivered is decisive for the nestling's survival (Newton 1979). Raptors are single-prey loaders, and therefore prefer larger prey for transport to the nest compared to what they consume at the capture site, because this reduces the relative cost of transportation (Sonerud 1992). Optimal foraging theory explains how predators should select their prey to maximize net energy intake per time unit (Stephens & Krebs 1986 and references therein). Several small prey items are needed to obtain the equal amount of energy as one large prey item. However, for larger prey, there is a longer handling time, and less portion of the prey is edible (Slagsvold & Sonerud 2007; Slagsvold et al. 2010). Throughout the breeding season, raptors are constrained to the nest location and in the need of rapid returns to the hunting areas in order to satisfy the nestlings dietary requirements (Sonerud 1992).

The golden eagle (*Aquila chrysaetos*), is regarded as an opportunistic raptor at the top of the food chain (Sulkava et al. 1999; Watson 2010). It is a widespread bird breeding through large parts of Norway, and its favoured habitat is open forest, mountain areas and islands along the coast (Gjershaug & Nygård 2003). To locate its prey, the golden eagle needs open mountainous landscape, because the eagle mostly discover its prey by searching from the air (Watson 2010). Prey items are usually captured on the ground (Watson 2010). The breeding population of the golden eagle in Norway during 2010-2014, was estimated to be 963 breeding pairs (Dahl et al. 2015). The number of golden eagles pairs have increased after the protection in 1968, and after levels of organochlorine pesticides became lower (Nygård & Polder 2012). The golden eagle has the status Least Concern (LC) on the Norwegian Red List (Henriksen & Hilmo 2015). In Oppland County, 55-65 pairs of golden eagle resides here, 2014 was a peak year for the breeding population with 31 breeding eagles (Opheim & Høitomt 2014). The following year was as a poor year for the golden eagle, and only 14 breeding pairs were registered of the 43 known occupied territories in the County (G. Høitomt, pers. comm.).

Golden eagle takes a wide variety and size range of prey, and its diet has been investigated in numerous studies (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007; Watson 2010; Shafaeipour 2015). The diet varies from habitat to habitat and between individuals, and common prey are medium sized birds or mammals in the range 0.5-4 kg from the families (Leporidae), (Sciuridae), (Tetraonidae) and (Phasianidae) (Watson 2010). In Fennoscandia, the golden eagle has a wide food niche consisting of grouse (Tetraonidae), mountain hare (*Lepus timidus*), reindeer (*Rangifer tarandus*), Norwegian lemming (*Lemus lemmus*), field vole or root vole (*Microtus sp.*), red fox (*Vulpes vulpes*) and mustelids (Mustelidae), and around 30 bird species other than grouse have been recorded as prey (Tjernberg 1981; Nyström et al. 2006). Golden eagles predation on ungulates has been documented in several studies (Tjernberg 1981; Warren et al. 2001; Nyström et al. 2006; Johnsen et al. 2007; Watson 2010). Predation by the golden eagle on livestock is controversial (Warren et al. 2001; Gjershaug & Nygård 2003). In 2014 142 reindeers was documented killed by the golden eagle in Norway (Rovbase 2015). However, the number of compensated reindeers was 4499 (Rovbase 2015). Also for sheep (*Ovis aries*), there is a loss due to predation by golden eagle, and the Norwegian Nature Inspectorate documented 95 sheep killed by eagles in Norway in 2014. However, the County governors disbursed the same year compensation for 1665 sheep (Rovbase 2015).

Most studies on the diet of the golden eagle have been based on collecting prey remains and pellets, or on direct observations from a hide of prey items delivered at nest (Tjernberg 1981; Nyström et al. 2006; Johnsen et al. 2007). However, collecting pellets and prey remains appears to underestimate the total amount of food delivered, and bias the importance of prey groups (Simmons et al. 1991; Lewis et al. 2004; Tornberg & Reif 2007; Slagsvold et al. 2010; Watson 2010). Recently, video monitoring has been performed successfully at the nest on several raptors (Lewis et al. 2004; Steen 2009; Skouen 2012; Sonerud et al. 2014; Dihle 2015; Shafaeipour 2015). This method may give a better understanding of the variety of the diet, and a more precise estimate. Studies of the golden eagle diet conducted in Telemark County and Oppland County in Norway, by Skouen (2012) and Dihle (2015) respectively, have revealed that microtine rodents, especially Norwegian lemming, and smaller birds make up a more important part of the diet than estimated by studies based on only pellets and prey remains.

An understanding of which prey species is the most important in the diet of the golden eagle, is a key to strengthen the management and conservation strategies of the eagle and its prey species (Lewis et al. 2004; Watson 2010). Therefore in this study, I investigated the diet and prey handling of a breeding golden eagle pair in Oppland County, south Norway, by using video monitoring at the nest. Firstly, I wanted to derive the golden eagles’ diet during the breeding season, and reveal the most important prey species, including whether domestic sheep and lambs are delivered as prey on the nest. Secondly, I wanted to find variables that affect the parents’ prey handling and the nestling’s feeding behaviour.

Methods

Study area

The study was conducted in Gausdal municipality in Oppland County, located in south Norway at 61° 20´- 61° 40´ N; 9° 60` - 9° 80` E (exact position is confidential). The study area is in the border area of Gausdal Vestfjell, a mountain area east of Jotunheimen between Valdres and Gudbrandsdalen, with altitude varying from 550-1362 m. The fieldwork was conducted in May- July 2015. The area southeast of the nest is a valley with sparsely settled farms and agricultural land, with domestic sheep and cows (*Bos taurus*) grazing on pastures. There are also large forested areas, dominated by Norwegian spruces (*Pica abies*). At higher altitudes is a lush and species-rich low mountain region with a great variety of habitats. The mountain landscape consists of bare mountain parties, larger marsh and willow areas, and forested valleys. Above the coniferous forest is mainly mountain birch (*Betula pubescens ssp. czerepanovii*) forest close to the treeline, which is at an attitude of 1050 m (Rekdal 2002). Large parts of the western study area are qualified as areas without major infrastructure development, and include numerous streams, rivers, and lakes (Fylkesmannen i Oppland 2007). There are also many summer dairy farms still in use in the low alpine plateau, mainly used as grazing land for cows and sheep.

In this study, I have video monitored prey deliveries at one nest for 10 weeks. The nest is positioned on a cliff ledge in a mountainside facing east in a creek ravine. This is the same nest as filmed by (Dihle 2015), where the camera was installed in winter 2014, well before the breeding season, to minimize the disturbance of the birds (Dihle 2015). The camera was placed in a crack in the mountain wall above the nest, c. 1 m away. The golden eagles spend their lives in a limited area, where they have their nest and hunting range (Watson 2010). Because the eagle is highly territorial I assumed that the female and male that I filmed were the same individuals as filmed by Dihle (2015) and the same throughout the filming period. A comparison of the eagles on the video material from Dihle (2015) and my study confirmed this assumption.

The time of solar midday at the study locality was calculated to be 13.20 hours, and was the average of the solar midday when the recording started 15 May (13.14 h), and when the recording ended 26 July (13.24 h).

Video monitoring

Two nestlings hatched in early May, and the filming started when they were estimated to be 4-8 days old. As a reference, their age was set to 7 days on 15 May. After one day with recording the youngest of the nestlings died at the age 5-9 days. The monitoring continued until the nestling left the nest when the nest had been filmed for 71 days. One prey was recorded delivered at the nest, one day after the nestling fledged the nest.

The method used for filming was the same as described by Steen (2009). The camera used was a CCD (charged-coupled device) equipped with a wide-angle lens for better monitoring of the nest bed. The camera was connected with a 100 m video cable to a mini digital recorder (mini DVR) that stored the data on a SD card, which was changed once a week. The events were stored as video files (format .avi) on 32 GB SD cards. The recording equipment was placed in a waterproof container. The 100 m long cable was stretched away from the nest, so that the monitoring did not disturb the eagles. To provide power the equipment was connected to a 12 V battery and a solar cell panel. The mini DVR had a video motion detection sensor, which was triggered by movements. This made analysing the video material less time consuming. At each trigging, the camera recorded 5 s before each delivery or movement, and 10 s afterwards. The sensitivity of the sensor was set at a high level, to capture all deliveries and handling of prey. The resolution was 704 x 560 lines, and the frame rate was 25 pictures per s.

Prey availability

The local property management (Gausdal fjellstyre) has assessed the willow grouse population density in Gausdal Vestfjell each year since 1999. In 2015 there was a marked decrease in the willow grouse density compared with 2014, with c. 5.5 grouse per km^2 in 2015 and 11.0 per km^2 in 2014 (Hønsefuglportalen 2015). Also, 2015 was a low year for microtine rodents in the region (G. A. Sonerud, pers. comm.). Finally, the mountain hare population was characterised by local hunters to be lower than average in 2015. The access to potential livestock in the area is high, close to the nest location there are several farms, where sheep graze on enclosed pastures from early May. The sheep are released to outlaying fields for summer grazing in June (pers. obs).

Prey type, size and delivery rate

Analysis of all deliveries was displayed on a 49 inches TV monitor, either in slow speed or played frame by frame. The prey items delivered were identified to the lowest taxonomic level possible, and assigned to one of two main categories; birds or mammals. Most prey items were identified to species or genus. For each delivery, the sex of the parent that delivered the item was determined from morphological features and registered. For each prey item delivered the following variables were registered: the date and hour to the nearest minute, whether the prey item was decapitated or not, whether a part or less than the head was missing or not, and whether the prey, if avian, was plucked before delivery or not. Gross body mass for each prey was obtained from literature (Cramp & Perrins 1993a, b, 1994a, b; Frislid & Jensen 2004). For prey that was delivered decapitated the estimated mass of the head was subtracted, 16.5% for voles (Asakskogen 2003), and 12.9% for birds (T. Slagsvold & G. A. Sonerud, unpublished data). When other parts of the prey were missing, the prey mass was estimated visually. The body mass of a prey before it was captured by the eagle was termed gross body mass. The estimate of the prey items delivered at the nest was termed the net body mass.

Weather data

The data for ambient temperature (TMP) and precipitation (PPT) were taken from the climate database eKlima (2015) of the Norwegian Meteorological Institute. Gausdal- Follebu (13030) and Skåbu (13655) are the meteorological stations closest to my study area, and their altitude was 375 and 928 m above sea level, respectively. I selected Skåbu because it most likely reflected the weather in the area that the eagles hunted. Both stations measured ambient air temperature four times a day, and precipitation twice a day. All prey deliveries on the same day were given the same value for precipitation. Ambient temperature at delivery was interpolated linearly from the recorded temperature closest in time before and after delivery.

Statistical analysis

The statistical analysis and the construction of figures were conducted in JMP® version 12.1.0 (SAS 2015). All residuals were checked for normality. In order to find the models with the lowest Akaike's information (AIC), all ecological reasonable combinations were tested, and the model with the lowest AIC value was selected. Akaike weights were used to describe the probability that the candidate model was the best model (Wagenmakers & Farrell 2004). The most parsimonious model was investigated further if ΔAIC was ≤ 2.0 (Burnham 2002). Parameter estimates and their p-values from Wald test are presented for the model selected based on the best model from the AIC selection. The standard criterion of significance were α=0.05. Mean values are presented with one standard error.

Contingency analyses were used to test for relationship between main prey group (bird or mammal) and delivering parent (male or female), between prey group (mountain hare, thrush, willow grouse, or other) and delivering parent (male or female), and between three prey groups (mountain hare, thrush, and willow grouse) and whether the current prey delivered was the same as the previous (yes or no). After AIC model selection logistic regression by likelihood ratio tests was used to test the effects of different variables in the chosen models.

Results

Prey selection

A total of 71 prey items were recorded delivered at the nest during the study period. Of these, 43 items where identified to species level and 26 to genus. One bird could not be identified to species or genus, and one prey item could not be identified at all (Table 1). The diet was dominated by birds (67.6%), while the remaining portion were mammals (31.0%) or unidentified (1.4%). Mountain hare was the dominations prey species and accounted for 26.8% of delivered items and 67.4% of delivered net prey biomass. Thrushes (*Turdus sp.*) and willow grouse were the second and third most prevalent prey with 40.6% and 19.7% of delivered items respectively, but differed in net prey biomass, with 7.4% and 19.5%, respectively. Other prey represented only a small portion of the diet. Only one *Microtus* vole was delivered at the nest, and made up 1.4% of all recorded prey items delivered and less than 0.2% of net prey biomass (Table 1). No livestock was recorded delivered at the nest during the study period.

Prey deliveries

The mean (±SE) estimated gross body mass for all prey delivered, i.e. the body mass at the time of capture, was 912 ± 145 g. Estimated mean net body mass for all prey items delivered was 448 ± 68 g. Of the 71 prey items recorded, there were 48 birds, and their net body mass was 208 ± 32 g. Mean ambient air temperature for all prey deliveries at the golden eagle nest was 9.1 ± 0.68°C. The mean precipitation for days when the pair of golden eagle delivered a prey to the nest was 0.7 ± 0.35 mm. Mean time from solar midday for all prey delivered was 03:41 ± 00:17 h. The time between two prey deliveries reflects times since last prey, and was on average 25:15 ± 3:06 h.

Table 1. Prey delivered at a golden eagle nest in Oppland County, Norway, as recorded by video monitoring (78 days), with relative contribution per species (%), average estimated mass (g) net and gross, total prey mass net and gross, and % of estimated mass net and gross of prey in the diet.

Prey species	Prey number		Net body mass (g)			Gross body mass (g)		
	N	%	Per prey	All prey	%	Per prey	All prey	%
Willow grouse (*Lagopus lagopus*)	14	19.7	436[1]	6104	19.5	500	7000	12.0
Black grouse *(Tetrao tetrix*)	1	1.4	1132	1132	3.6	1300	1300	2.0
Short-eared owl (*Asio flammeus*)	1	1.4	380	380	1.2	380	380	0.6
Fieldfare (*Turdus pilaris*)	3	4.2	100	300	1.0	100	300	0.5
Song thrush (*Turdus philomelos*) or Redwing (*Turdus iliacus*)	5	7.0	70	350	1.1	70	350	0.6
Thrush indet. *(Turdus* sp.)	21	29.6	79[2]	1659	5.3	90	1890	3.0
Pipit *(Anthus* sp.)	1	1.4	20	20	0.1	20	20	0.3
Northern wheatear (*Oenanthe oenanthe*)	1	1.4	25	25	0.1	25	25	0.04
Willow warbler *(Phylloscopus trochilus*)	1	1.4	10	10	0.03	10	10	0.02
Bird indet.	1	1.4	100	100	0.3	100	100	0.2
Birds total	48	67.6	208	10080	31.9	235	11375	17.7
Mountain hare (*Lepus timidus*)	19	26.8	1111[3]	21109	67.4	2753	52307	83.0
Field vole or root vole *(Microtus* sp.)	1	1.4	50	50	0.2	50	50	0.1
Stoat (*Mustela erminea*)	1	1.4	100	100	0.3	100	100	0.2
Mammals total	22	31.0	970	21259	68.1	2389	52457	82.4
Undefined	1	1.4						
Total	71	99.9		31339	100.0		63832	100.0

[1] Mean estimate, variation 250-500 g.

[2] Mean estimate, variation 30-87 g.

[3] Mean estimate, variation 100-2500 g.

Prey delivery by the parents

The male delivered a larger proportion (57%) of prey items to the nestling than the female. Birds (69%) were the most common prey group delivered at the nest by the male. The female delivered a marginally larger proportion of mammals to the nest (55%), but this difference was not significant (Figure 1). For both parents, the most active part of the day was after solar midday, with 54% of all prey deliveries.

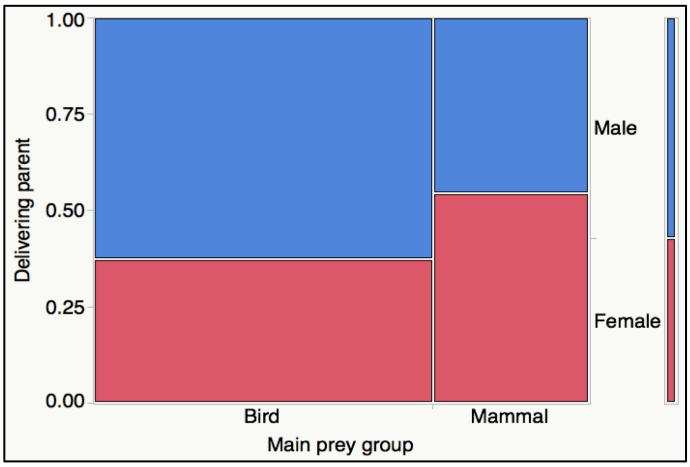


Figure 1. The distribution of the delivering parent on main prey group (bird or mammal) delivered at the golden eagle nest. Whole model: N= 70, χ^2= 1.78, df= 1, p= 0.18.

The male delivered 69% of all thrushes and 64% of all willow grouse, and 42% of the hares and 43% of other prey (Figure 2). However, these differences were not significant (Figure 2).

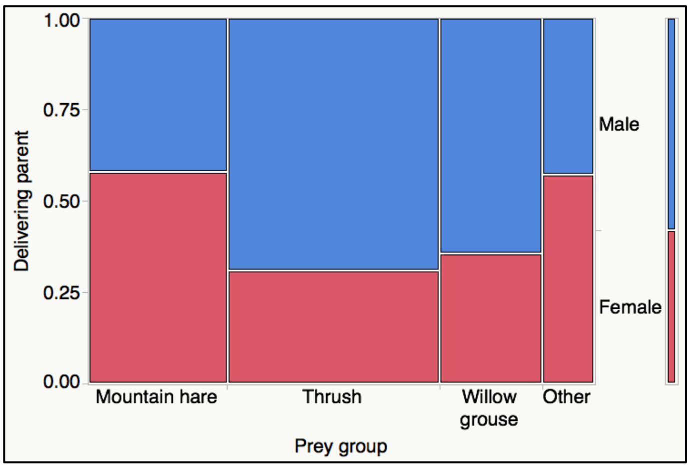


Figure 2. The distribution of the delivering parent on prey group (willow grouse, thrush, mountain hare or other prey) delivered at the golden eagle nest. Whole model: N= 69, χ^2= 4.30, df= 3, p= 0.23.

Prey handling

Potential factors affecting the probability that the nestling fed unassisted, using female feeding as reference level, were its age, net prey body mass, and whether the item was a bird or a mammal. Based on Aikaike weights (Table 2), model 1 and model 2 were likely to be the best models. However, because they both were heavily under-dispersed, with a low model fit (x^2 /df = 0.15), they were both disregarded. Model 3 (x^2/df = 0.32) was therefore chosen to be tested further. Model 3 included the variables main prey group, net prey body mass, nestling age, and the interaction between net prey body mass and main prey group (Table 2).

Table 2. Selection of models of factors affecting the probability that the golden eagle nestling fed unassisted rather than being fed by the female, with AIC values for the ten most supported models, together with ΔAIC values, and AIC weight. For main prey group, the estimates are calculated for birds with mammals as reference level.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Nestling age + net prey body mass + net prey body mass * nestling age	3	20.58	0.00	0.723
2	Nestling age + net prey body mass + net prey body mass * nestling age + main prey group	4	22.52	1.94	0.274
3	Nestling age + main prey group + net prey body mass + net prey body mass * main prey group	4	32.74	12.16	0.002
4	Nestling age + net prey body mass	2	35.49	14.91	< 0.001
5	Nestling age + main prey group + net prey body mass	3	37.21	16.63	< 0.001
6	Nestling age + main prey group	2	46.69	26.11	< 0.001
7	Nestling age	1	48.20	27.62	< 0.001
8	Main prey group + net prey body mass + net prey body mass * main prey group	3	58.20	37.62	< 0.001
9	Net prey body mass	1	60.76	40.18	< 0.001
10	Main prey group + net prey body mass	2	62.59	42.01	< 0.001

The probability that the female fed the nestling significantly decreased as the nestling aged (Table 3). During the nestling period, only the female fed the nestling. After 41 days, the nestling fed unassisted for the first time. The model predicted that when the nestling was 49 days old, it was as likely to feed unassisted as to be fed by the female (Figure 3). Thereafter, progressively more of the food consumed by the nestling was self-fed (Table 3). In total, the nestling fed unassisted on the majority (60%) of the prey items (Figure 3). Net prey body mass significantly affected the probability that the nestling fed unassisted (Table 3). Still, the female kept feeding the nestling occasionally until fledging.

Most prey items fed by the female to the nestling were large mammals (Figure 4a). Whether a prey item delivered at the nest was fed with assistance from the female, was significantly affected by the interaction between main prey group and net prey body mass (Table 3). The effect of net prey body mass on the probability that the female was feeding the nestling differed between birds and mammals (Figure 4a, b). The nestling was less likely to consume prey items unassisted as prey items became larger, but that effect differed between avian and mammalian prey (Figure 4a, b).

Table 3. Parameter estimates from Wald test for the selected model (model 3) of variables affecting the probability that the golden eagle nestling fed unassisted rather than being fed by the female, based on likelihood ratio tests in a logistic regression. For main prey group, the estimates are calculated for birds with mammals as reference level. Whole model (log likelihood ratio test): N= 69, χ^2= 71.40, df= 4, p< 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	6.594	2.793		5.57	0.018
Nestling age	-0.174	0.054	1	10.24	0.0014
Net prey body mass	0.008	0.002	1	10.25	0.0014
Main prey group	0.945	0.788	1	1.44	0.23
Main prey group * net prey body mass	0.005	0.002	1	4.99	0.025

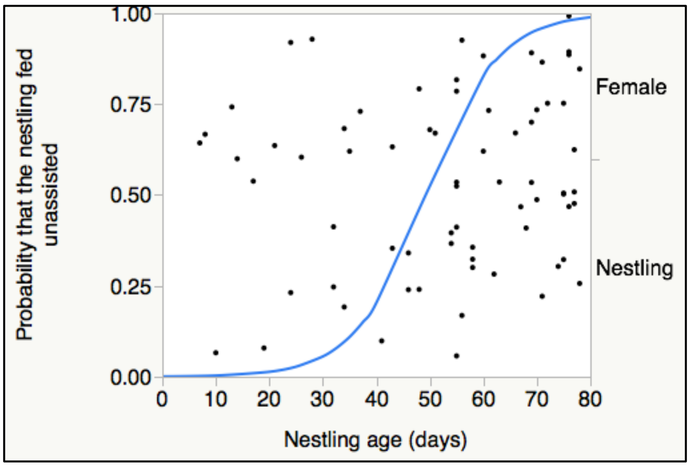
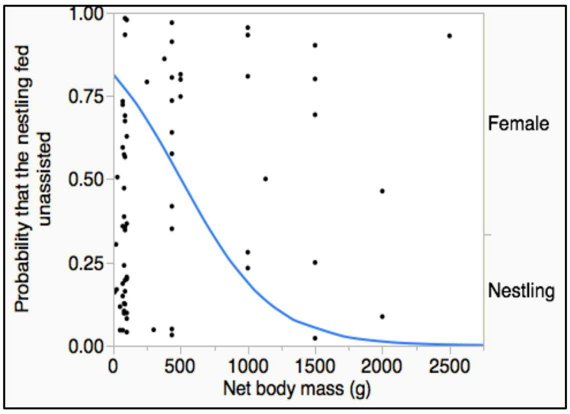


Figure 3. The probability that the golden eagle nestling fed unassisted, as a function of nestling age. Whole model: N= 70, χ^2= 50.21, df= 1, p< 0.0001.

a)



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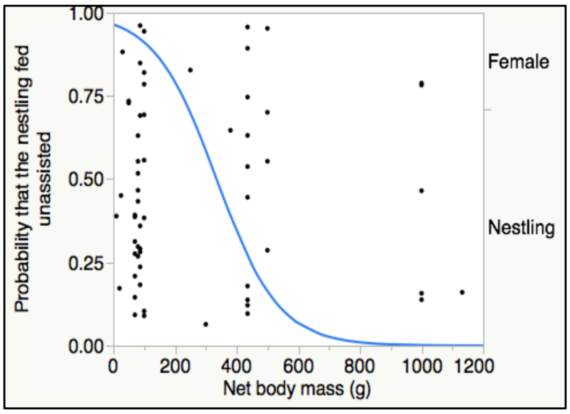

Figure 4. The probability that the golden eagle nestling fed unassisted as a function of the net body mass (g) of prey deliveries. a) Mammals: Whole model: N= 21, χ^2= 10.45, df= 1, p= 0.0012.
b) Birds: Whole model: N= 48, χ^2= 24.66, df= 1, p< 0.0001.

Selection of mountain hare as prey

Potential factors affecting the probability of a prey item delivered being a mountain hare rather than other prey were time from solar midday, precipitation, ambient temperature, and nestling age. Based on Aikaike weights (Table 4), model 1 was only 1.1 times more likely to be the best model than model 2, which is a more parsimonious model, and therefore both models were tested further. Model 1 included the variables time from solar midday, ambient temperature, and precipitation, while model 2 included nestling age and precipitation (Table 4).

Table 4. Selection of models of factors affecting the probability of a prey item delivered being a mountain hare or another prey, with AIC values for the ten most supported models, together with ΔAIC and AIC weight. The variables ambient air temperature and precipitation are abbreviated TMP and PPT, respectively.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Time from solar midday + PPT + TMP	3	78.35	0.00	0.195
2	Nestling age + PPT	2	78.55	0.20	0.176
3	Nestling age + time from solar midday + PPT	3	79.31	0.96	0.120
4	Time from solar midday + PPT	2	79.32	0.97	0.120
5	PPT	1	79.63	1.28	0.103
6	Nestling age + time since last delivery + PPT + TMP	4	79.97	1.62	0.087
7	Nestling age + PPT + TMP	3	80.07	1.72	0.082
8	Nestling age	1	80.61	2.26	0.063
9	Nestling age + time from solar midday	2	82.27	3.92	0.027
10	Nestling age + TMP	2	82.30	3.95	0.027

In model 1, the effect of precipitation was significant, while the effects of ambient temperature and time from solar midday were marginally significant (Table 5). In model 2, the effects of both variables, i.e. precipitation and nestling age, were marginally significant (Table 6). The probability that the prey delivered to the nest was a mountain hare declined with increasing precipitation (Figure 5, Tables 5 and 6), and with increasing nestling age (Figure 6). The probability that a mountain hare was delivered to the nest tended to decline with increasing ambient temperature and time from solar midday (Table 5).

Nestling age can be considered as a proxy for season, because it is possible to calculate the nestling age based on time and date from the recordings. Consequently, it is possible to state that the deliveries of mountain hare mainly occurred early in the season, as nestling age zero is approximately 8 May. The deliveries of hare decreased rapidly in June and July, until the nestling fledged 25 July, 78 days old (Figure 6).

Table 5. Parameter estimates from Wald test for the most supported model (model 1) of variables affecting the probability that a prey delivered at the golden eagle nest was a hare rather than other prey, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 70, χ^2= 12.12, df= 3, p= 0.0070.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	1.376	0.872		2.49	0.11
Time from solar midday	-0.249	0.133	1	3.49	0.062
Temperature	-0.092	0.055	1	2.86	0.091
Precipitation	-0.399	0.190	1	4.42	0.036

Table 6. Parameter estimates from Wald test for the second most supported model (model 2) of variables affecting the probability that a prey delivered at the golden eagle nest was a hare rather than other prey, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 70, χ^2= 9.67, df= 2, p= 0.0079.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	0.651	0.708		0.85	0.36
Precipitation	-0.298	0.175	1	2.90	0.089
Nestling age	-0.024	0.014	1	3.22	0.073

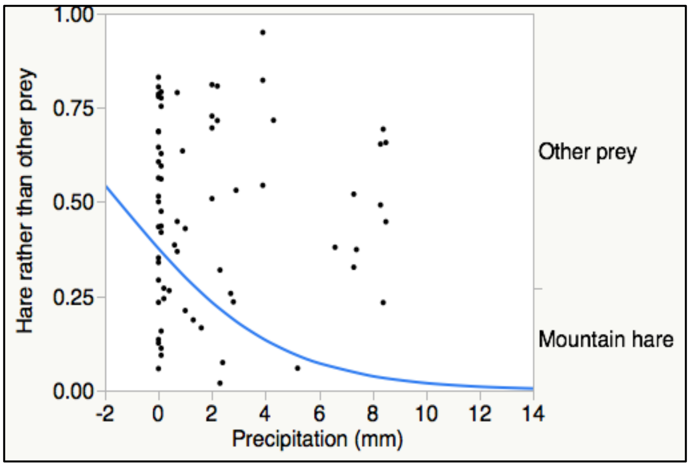

Figure 5. The probability that the prey delivered at the golden eagle nest was a hare rather than other prey as a function of precipitation. Whole model: N= 70, χ^2=6.35, df= 1, p= 0.012.

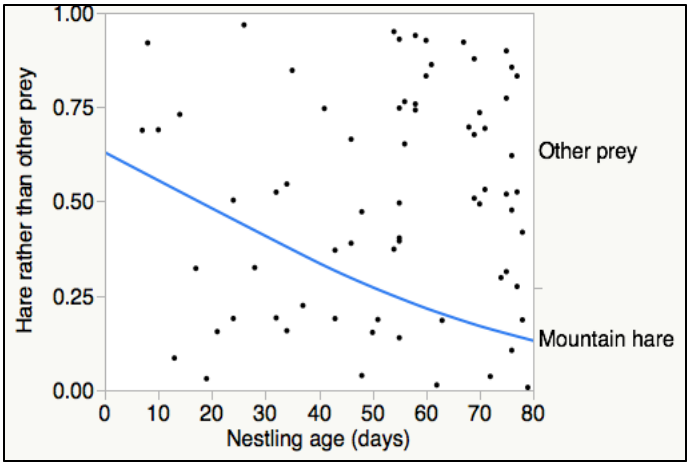

Figure 6. The probability that the prey delivered at the golden eagle nest was a hare rather than other prey as a function of nestling age. Whole model: N= 70, χ^2=5.43, df= 1, p= 0.020.

Selection of thrushes as prey

Potential factors affecting the probability of a prey item delivered being a thrush rather than other prey were precipitation, ambient temperature, time since last delivery, and nestling age. Based on Aikaike weights (Table 7), model 1 is almost twice (1.92) as likely to be the best model as model 2, which is a more parsimonious model, and therefore both models are tested further. Model 1 included two variables precipitation and nestling age, while model 2 included only nestling age (Table 7).

Table 7. Selection of models of factors affecting the probability of a prey item delivered being a thrush or another prey, with AIC values, ΔAIC, and AIC weight for the ten most supported models. The variables ambient air temperature and precipitation are abbreviated TMP and PPT, respectively.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Nestling age + PPT	2	82.14	0.00	0.295
2	Nestling age	1	83.44	1.30	0.154
3	Nestling age + PPT + TMP	3	83.61	1.47	0.142
4	Nestling age +time since last delivery + PPT	3	83.75	1.61	0.132
5	Nestling age +time since last delivery	2	84.65	2.51	0.084
6	Nestling age +time since last delivery + PPT + TMP	4	84.90	2.76	0.074
7	Nestling age + TMP	2	85.12	2.98	0.067
8	Nestling age +time since last delivery + TMP	3	85.92	3.78	0.045
9	PPT	1	90.91	8.77	0.004
10	PPT + TMP	2	91.00	8.86	0.004

The effect of precipitation was marginally significant (Table 8). The probability that a thrush were delivered at the nest increased with a higher amount of precipitation (Figure 7).

Nestling age had a significant effect on the probability of a prey delivered to the nest being a thrush (Tables 8 and 9). The probability that the prey delivered was a thrush rather than other prey increased significantly with nestling age. When regarding nestling age as a proxy for season, a prey item delivered was more likely a thrush later in the season (Figure 8).

Table 8. Parameter estimates from Wald test for the most supported model (model 1) of variables affecting the probability that a prey delivered at the golden eagle nest was a thrush rather than an other prey, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 69, χ^2= 18.13, df= 2, p< 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	P
Intercept	3.429	1.025		11.2	0.0008
Precipitation	-0.187	0.104	1	3.21	0.073
Nestling age	-0.049	0.017	1	8.43	0.0037

Table 9. Parameter estimates from Wald test for the second most supported model (model 2) of variables affecting the probability that a prey delivered at the golden eagle nest was a thrush rather than an other prey, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 69, χ^2= 14.63, df= 1, p< 0.0001.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	3.309	0.994		11.07	0.0009
Nestling age	-0.054	0.017	1	10.72	0.0011

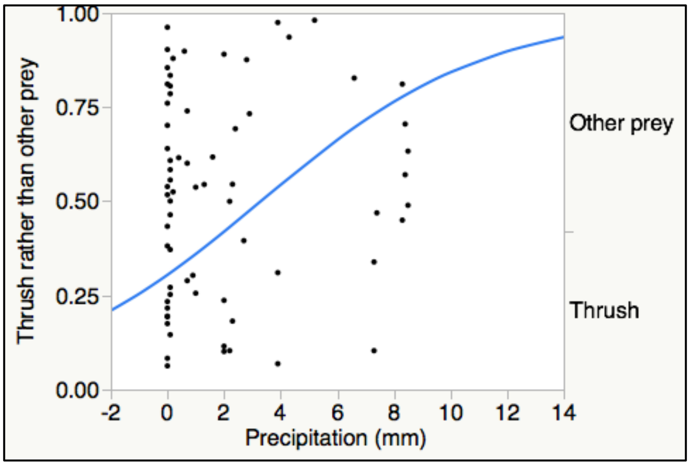

Figure 7. The probability that the prey delivered at the golden eagle nest was a thrush rather than other prey as a function of precipitation. Whole model: N= 69, χ^2=7.16, df= 1, p=0.0075.

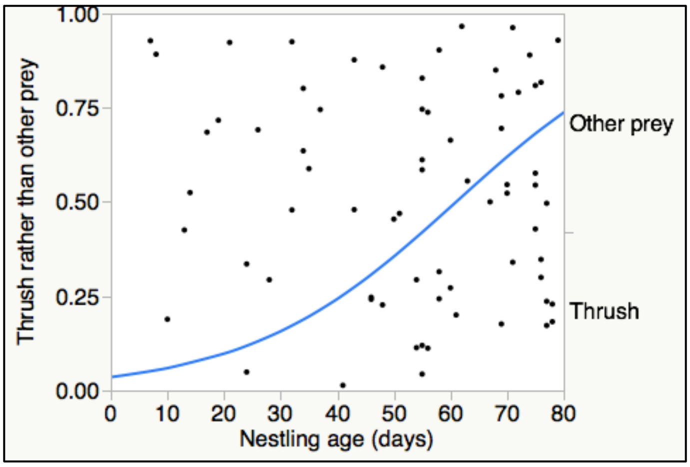

Figure 8. The probability that the prey delivered at the golden eagle nest was a thrush rather than other prey as a function of nestling age. Whole model: N= 69, χ^2=14.63, df= 1, p< 0.0001.

Selection of willow grouse rather than other prey

Potential factors affecting the probability of a prey item delivered being a willow grouse rather than other prey were time from solar midday, precipitation, whether the delivery took place before or after midday, and nestling age. Based on Aikaike weights (Table 10), model 1 is twice (2.1) as likely to be the best model as model 2. Model 1 included only the variable nestling age.

Table 10. Selection of models of factors affecting the probability of a prey item delivered being a willow grouse rather than other, with AIC values, ΔAIC, and AIC weight for the for the ten most supported models. The variable precipitation are abbreviated PPT.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Nestling age	1	71.01	0.00	0.271
2	Nestling age + before or after midday	2	72.52	1.51	0.127
3	Nestling age + time from solar midday	2	72.94	1.93	0.103
4	Before or after midday	1	72.95	1.94	0.103
5	Nestling age + PPT	2	73.06	2.05	0.097
6	PPT	1	73.78	2.77	0.068
6	Time from midday	1	73.78	2.77	0.068
7	Nestling age + time from solar midday + before or after midday	3	74.50	3.49	0.047
8	Nestling age + before or after midday + PPT	3	74.63	3.62	0.044
9	Nestling age + time from solar midday + PPT	3	74.94	3.93	0.038
10	Before or after midday + time from solar midday	3	75.14	4.13	0.034

The probability that an item delivered was a willow grouse rather than an other prey was marginally significantly affected by nestling age, with negative effect (Table 11).

Table 11. Parameter estimates from Wald test for the most supported model (model 1) of variables affecting the probability that a prey delivered at the nest was a willow grouse rather than thrush, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 69, χ^2= 2.77, df= 1, p= 0.096.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-0.194	1.154		0.07	0.79
Nestling age	-0.024	0.020	1	2.75	0.097

Selection of willow grouse rather than thrush

Potential factors affecting the probability of a prey item delivered being a willow grouse rather than thrush were time from solar midday, ambient temperature, time since last delivery, and nestling age. Based on Aikaike weights (Table 12), model 1 is one and a half times (1.5) as likely to be the best model than model 2. Model 1 included only the variable nestling age (Table 12).

Table 12. Selection of models of factors affecting the probability of a prey item delivered being a willow grouse rather than thrush, with AIC values, ΔAIC and AIC weight for the ten most supported models. The variable ambient air temperature are abbreviated TMP.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Nestling age	1	49.91	0.00	0.284
2	Nestling age + time since last delivery	2	50.72	0.81	0.189
3	Nestling age + time since last delivery + TMP	3	51.54	1.63	0.126
4	Nestling age + TMP	2	51.66	1.75	0.118
5	Nestling age + time from solar midday	2	51.85	1.94	0.108
6	Nestling age + time since last delivery + time from solar midday	3	52.58	2.67	0.075
7	Nestling age + time since last delivery + time from solar midday + TMP	4	53.89	3.98	0.039
8	Nestling age + time from solar midday + TMP	3	53.90	3.99	0.039
9	Time since last delivery	1	55.95	6.04	0.014
10	TMP	1	56.62	6.71	0.010

The probability that an item delivered was a willow grouse rather than a thrush was significantly affected by nestling age (Table 13). With increasing nestling age, (and later in the season) the probability of willow grouse as compared to thrush decreased rapidly (Figure 9).

Table 13. Parameter estimates from Wald test for the most supported model (model 1) of variables affecting the probability that a prey delivered at the nest was a willow grouse rather than a thrush, based on likelihood ratio tests in a logistic regression. Whole model (log likelihood ratio test): N= 43, χ^2= 8.66, df= 1, p= 0.0033.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	-2.143	1.154		3.44	0.063
Nestling age	0.052	0.020	1	6.74	0.0094

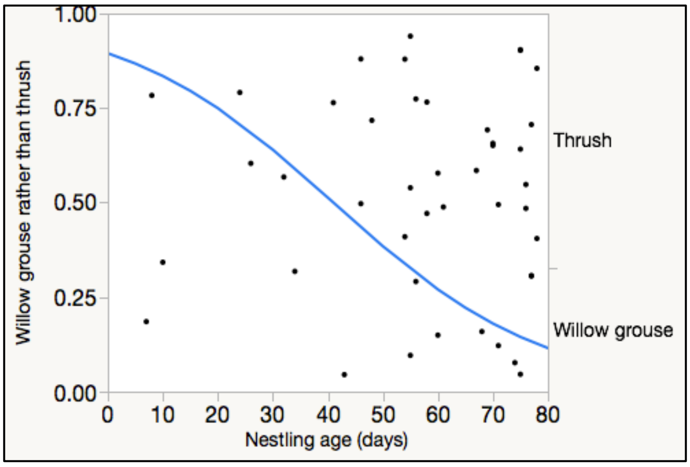

Figure 9. The probability that the prey delivered at the golden eagle nest was a willow grouse rather than thrush as a function of nestling age. Whole model: N= 43, χ^2=8.66, df= 1, p= 0.0033.

Win-stay or win-shift hunting strategy

Potential factors affecting the probability that the current (N) prey item delivered at the golden eagle nest was of the same type as the previous (N-1) prey item were prey group, time from solar midday, time since last delivery, and ambient temperature. Before the analysis, all prey items other than mountain hare, thrush, and willow grouse were excluded. Based on Aikaike weights (Table 14), model 1 is almost 1.8 times as likely to be the best model as model 2. Model 1 included the variable prey group (Table 14).

Table 14. Selection of models of factors affecting the probability that the current (N) prey item delivered at the golden eagle nest was of the same type as the previous (N-1) prey item, with AIC values, ΔAIC and AIC weight for the ten most supported models. The variable ambient air temperature are abbreviated TMP.

Model no.	Variables	df	AIC	ΔAIC	AIC-weight
1	Prey group	2	76.89	0.00	0.256
2	Prey group + time from solar midday	3	78.01	1.12	0.146
3	Prey group + TMP	3	78.40	1.51	0.120
4	Prey group + time since last delivery	3	78.66	1.77	0.105
5	Prey group + time from solar midday + TMP	4	78.95	2.06	0.091
6	Prey group + time since last delivery + TMP	4	79.71	2.82	0.062
7	Prey group + time since last delivery + time from solar midday	4	79.79	2.90	0.060
8	Prey group + time since last delivery + time from solar midday + TMP	5	79.89	3.00	0.057
9	Time since last delivery	1	80.02	3.13	0.053
10	Time from solar midday	1	80.20	3.31	0.049

The probability that a prey item delivered at the nest (N) was of the same type as the previous (N-1) prey item differed significantly between thrush and willow grouse, but not between mountain hare and willow grouse (Table 15). The probability that a prey item delivered at the nest (N) was the same species as the previous (N-1) prey item was 52% for thrush, 26% for mountain hare, and 15% for willow grouse (Figure 10).

Table 15. Parameter estimates from Wald test for the most supported model (model 1) of variables affecting the probability that the current (N) prey item delivered at the golden eagle nest was of the same type as the previous (N-1) prey item, based on likelihood ratio tests in a logistic regression. All prey items other than mountain hare, thrush, and willow grouse were excluded from the analysis. Whole model (log likelihood ratio test): N= 59, χ^2= 6.37, df= 2, p= 0.041.

Explanatory variables	Estimate	SE	df	χ^2	p
Intercept	0.887	0.335		7.00	0.008
Prey group (Mountain hare vs. willow grouse)	0.143	0.450	1	0.10	0.75
Prey group (Thrush vs. willow grouse)	-0.961	0.402	1	5.71	0.017

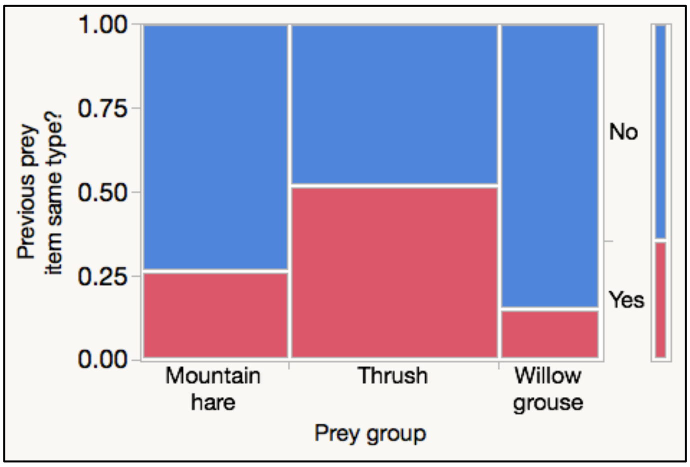

Figure 10. The probability that the current (N) prey delivered at the golden eagle nest was of the same type as the previous (N-1) prey item, when all prey items other than mountain hare, thrush, and willow grouse were excluded from the analysis. Whole model: N= 59, χ^2= 6.37, df= 2, p= 0.041.

Current prey thrush when previous prey thrush

For thrushes delivered, the probability that the previous prey item delivered also was a thrush declined significantly as the time since previous delivery increased (Figure 11). For willow grouse and hare there was no corresponding effect of time elapsed since the previous delivery.

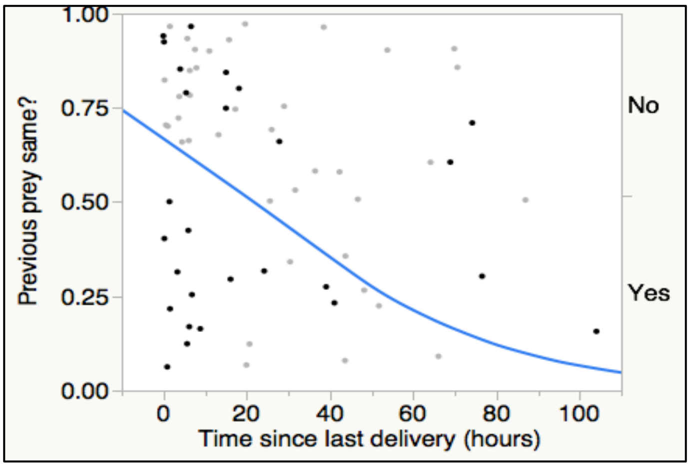

Figure 11. The probability that the current prey delivered at the golden eagle nest was the same as the previous prey delivered, as a function of time since last delivery, when all prey items other than thrush are excluded from the data. Whole model: N= 27, χ^2= 4.12, df= 1, p= 0.042.

Discussion

Diet during the nestling period

I found that the main prey species of the golden eagles were mountain hare and willow grouse. This was in accordance with other studies conducted in Fennoscandia, (Tjernberg 1981; Sulkava et al. 1999; Nyström et al. 2006; Johnsen et al. 2007). Numerically, the diet consisted of twice as many avian prey (68%) as mammalian prey (31%). In terms of biomass, mountain hare was the main prey species, making up 67% of the total biomass delivered. Willow grouse and thrushes were the second and third most important prey species in term of biomass, and accounted for 20% and 7% of the biomass, respectively. A surprisingly high number of the prey items delivered were thrushes (41%). This differs from earlier studies, where thrushes were almost absent (Tjernberg 1981; Sulkava et al. 1999; Nyström et al. 2006; Johnsen et al. 2007). However, the few studies that have used video monitoring in the same way as my study, found a high proportion of thrushes in the diet (Skouen 2012; Dihle 2015).

I registered 20% of the prey items delivered as *Lagopus* sp. The previous year Dihle (2015) found barely 1% *Lagopus* sp. among prey items at the same nest. Willow grouse is in several studies (Tjernberg 1981; Sulkava et al. 1999; Nyström et al. 2006; Johnsen et al. 2007) referred to as a preferred and important prey species of the golden eagle. Line transect counts of the willow grouse population in the mountain area west of the nest that I and Dihle (2015) studied, found a marked decrease in the willow grouse population density from 2014 to 2015, with approximate 11.0 grouse per km^2 in 2014 and to 5.5 per km^2 in 2015 (Hønsefuglportalen 2015). The low willow grouse estimate for 2015 may be a result of a low chick production, caused by a late spring, cold weather, or the absence of microtine rodents. From the decline in the grouse densities from 2014 to 2015 one would expect that the number of delivered *Lagopus* sp. would be lower in 2015 then 2014. To the contrary, the *Lagopus* sp was the third most important prey by number in my study.

I registered only one *Microtus* vole delivered at the nest, and this differ highly from 2014, when 50% of the prey items delivered at the same nest were microtine rodents (Dihle 2015). The regional microtine rodent populations fluctuate with 3-4 years cycles, and the population had a very high peak in 2014 and crashed to a low in 2015 (G. A. Sonerud, pers. comm.). The large difference between delivered microtine rodents in my study and Dihle's (2015) may indicate a functional response to microtine rodents, and not to willow grouse, because the grouse population was higher in 2014, which was the peak year of microtine rodents. On the other hand, it is also possible that the overall prey abundance during my study was lower than in 2014, as the low golden eagle breeding success in Oppland may indicate. The eagles may have used considerably more time searching for prey in 2015 than in 2014. Consequently, they would include less profitable prey in the diet, as optimal foraging theory predicts (MacArthur & Pianka 1966; Pulliam 1974; Stephens & Krebs 1986). An other factor behind the high level of grouse in the diet in 2015 compared to 2014 may be the late spring in 2015, which may have exposed the cryptic grouse to predators if grouse changed from winter plumage to summer plumage when the ground was still snow-covered.

In my and Dhile's (2015) study, there were no relationship between the assessed willow grouse population in the area and the number of grouse delivered by the golden eagles to the nest. Also, Skouen (2012) registered a high number of willow grouse in the diet, in spite that grouse population estimates in the area revealing a low population size. On the other hand, Watson (2010) stated that the number of grouse detected during transect counts in one year is a relative good estimator of the number of grouse (all species) in the diet. To better understand how the grouse population influences on the golden eagles, and what determines the proportion of grouse in the diet, weekly estimates of the grouse population should be conducted during the golden eagle nestling period.

The importance of small prey species in the diet of the golden eagle is poorly understood. Some researchers have claimed that small passerines and microtine rodents are fed to the nestlings only when larger prey is sparse (Steenhof & Kochert 1988; Sulkava et al. 1999). Tjernberg (1983) concluded that the breeding success of the golden eagle was affected by variations in the abundance of larger prey species, such as grouse and hare. Therefore, Tjernberg (1983) considered the fluctuations in the microtine rodent populations as a buffer against predation on small game species. Furthermore, Tjernberg (1983) and Gjershaug (1996) claimed that the offspring production of the golden eagle fluctuated with the microtine rodent abundance, with one year delay. This was also supported by Moss et al. (2012), who found that the proportion of territories with nestlings were affected by the abundance of grouse and hare, and the number of voles in the previous autumn. Dihle (2015), on the other hand, argued that the golden eagle responds functionally to microtine rodents, and that this may affect the golden eagle reproduction success directly. This is also in consistence with other findings (Nyström et al. 2004, 2006). According to Tjernberg (1983) and Moss et al.

(2012), 2015 should have been a good reproduction year for the golden eagle in Oppland County because 2014 was a peak year for microtine rodents. However, 2015 was a year with low golden eagle reproduction in Oppland County, that followed a peak year in the local golden eagle population in 2014 (G. Høitomt, pers. comm.). This supports Dihle's (2015) suggestion that golden eagles respond functionally to microtine rodents. If the diet analyses from both my study and that of Dihle (2015) are representative for other nests in Oppland County, there would be a positive relationship between the breeding success of golden eagle and rodent population density. In 2014, a high breeding rate for golden eagle and a peak year of microtine rodents were registered. The low breeding rate in 2015 corresponded with a registered low year for microtine rodents, which suggests a functional and numerical response to the microtine rodent population in the golden eagles. However, there may be differences between the study areas, as Tjernbergs's (1983) and Moss' et al. (2012) studies were conducted in boreal forests in Sweden. Additionally, there may be local variations in diets of nesting pairs of golden eagles, so that the diet analysis of only one nest from each year may not be sufficient to reflect the true diet of the population.

During the video recording period, no deliveries of sheep, or of body parts of sheep, were registered at the nest that I studied. This in accordance with other studies based on video monitoring (Skouen 2012; Dihle 2015). Sheep and lambs were released on summer grazing close to the nest both in my study, and those of Skouen (2012) and Dihle (2015). Although sheep occurred as carrion and live prey close to eagle nests in Scotland, carrion of sheep was still an uncommon prey in the nestling period (Watson 2010). There is reason to believe that the eagles had access to carrion of sheep close to all the nests studied in Norway. Why the eagles did not deliver any carrion or killed sheep may be due to difficulties to transport large prey items to the nests, and that carrion from large prey items could miss important elements, such as calcium, that influences the nestlings growth negatively (Watson 2010). In contrast to studies based on video monitoring, Warren et al. (2001) in northern Norway found that golden eagles were responsible for the death of five out of 253 lambs with mortality transmitters. However, it was not proven that breeding eagles were responsible for the killings. In Gausdal municipality, where my study nest was located, compensation for 22 lambs was disbursed in 2014 (Rovbase 2015). In this municipality there are four pair of golden eagles (Opheim & Høitomt 2014). Warren et al. (2001) recorded sheep killed by the golden eagle in the early summer months. Later in the season all the carrion that the golden eagle was registered to feed on was killed by other predators (Warren et al. 2001). Other studies also have concluded that the golden eagle predation on sheep is most common in May and June (Loland 2014). Early in the season the lambs are small, and would be an easier target for the golden eagle. Therefore, video monitoring at the nest early in the season should be a suitable method to record potential deliveries of sheep. The golden eagle's impact on livestock is a source of conflict, and Heggøy & Øien (2014) identify several weaknesses in the Norwegian documentation system for sheep and reindeer predation. In addition, there is a lack of documentation. Together this gives the golden eagle an undeserved bad reputation as predator on livestock (Heggøy & Øien 2014). In Norway the number of sheep reported killed, is apparently not related to the size of the golden eagle population (Gjershaug & Nygård 2003).

The average gross mass of prey at the time of capture, in my study, was estimated to be 912 g. However, the average net mass of prey delivered at the nest in 2015 was 448 g. The latter is similar to the net body mass calculated from Skouen (2012) and Dihle (2015), being 493 g and 422 g respectively. The golden eagle's prey spans from small passerine birds to large species such as the mountain hare. The typically range in size is estimated to be 0.5-4 kg (Watson 2010; Schweiger et al. 2015). For northern parts of Europe, the most common body mass class of prey is estimated to be 0.5-2 kg (Watson 2010). The difference in gross and net body mass of almost 0.5 kg in my study i.e. a doubling of the estimated body mass, may be due to deliveries of mountain hare at the nest, because eagles often only bring one leg, half of the hare, or juvenile hares back to the nest (pers. obs). Studies without video monitoring, would register a prey remain of hare as one whole hare delivered at the nest. Video monitoring, on the other hand, record the actual size of the prey delivered, and therefore gives a more precise estimate of the prey body mass. My study therefore suggests that the typically body mass range for prey items could be between 0.4-1 kg for golden eagles in south Norway. However, this is extracted from only one nest in two seasons, and therefore more studies with video monitoring in different areas must be conducted to assess this suggestion further.

Diet studies on raptors have mainly been conducted in the nesting season, because the birds activity then is concentrated to the nest, where data can be easily collected (Lewis et al. 2004; Tornberg & Reif 2007). Studies of food habits in the other stages of the eagles' life would be much more difficult to conduct (Newton 1979). Collecting pellets and prey remains has been a common method to analyse the diet of the golden eagle and other raptors (Nyström et al. 2006; Johnsen et al. 2007). Diet analysis based on collection of uneaten food remains and pellets has several biases, e.g. the prey may not be discovered, different remains are preserved in the nest unequally, larger prey is easier to discover, prey body mass and time of prey delivery are hard to define, birds are overestimated in prey remains, and mammals are overestimated in pellets (Mersmann et al. 1992; Redpath et al. 2001; Lewis et al. 2004; Tornberg & Reif 2007). These biases may lead to a biased estimate of the eagle's true diet, and this may explain why many studies have found a large proportion of large prey species, and few smaller prey species. My study revealed a large proportion of passerine birds in the diet, which fits with results from other studies based on video monitoring (Skouen 2012; Dihle 2015). Video monitoring should therefore be regarded as a more reliable tool to analyse a raptors' diet during the nestling period than traditional analysis of prey remains and pellets (Lewis et al. 2004).

Prey handling

During the first 41 days of the nestling period, the nestling was entirely dependent upon the female to ingest food, which is eleven days more than found by Watson (2010), and 13 days more than observed by Dihle (2015). This may be due to a larger portion of avian prey and larger mammals in this study compared to Dihle (2015), where half of the delivered prey items were microtine rodents. Steen et al. (2010) found that the probability of voles and birds being decapitated before delivery to nests of Eurasian kestrel (*Falco tinnunculus*) increased with prey body mass and nestling age. Further, they also found that birds delivered were decapitated more often than voles, partly because birds were heavier than voles (Steen et al. 2010). Small prey animals, including voles, is preferred by the kestrel because they are easier to ingest (Steen et al. 2010). Dihle (2015) found that the nestling fed unassisted at an earlier age than in my study, probably because of an higher proportion of microtine rodents in the diet compared to my study, which had a high delivery rate of birds. However, the predicted age at which the nestling was as likely to feed unassisted as to be fed by the female, differed only with two days, and was 47 days in the study of Dihle (2015) and 49 days in my study.

I found that the nestling was feeding unassisted earlier on birds than on mammals, and that increasing net prey body mass decreased the probability that the nestling fed unassisted. While the latter finding fit with what other have found (Sonerud et al. 2014), the former is in contrast to what other studies have found, namely that small mammals have been fed unassisted by the nestling earlier than birds (Steen et al. 2010; Skouen 2012; Sonerud et al. 2013; Sonerud et al. 2014). Birds would be more difficult to handle than mammals of the same mass, due to protruding body parts such as bill, feathers, and long tarsi, and Slagsvold &

Sonerud (2007) have showed that the feeding time is longer for avian than for mammalian prey items of the same size. Passerine birds were observed swallowed whole by the nestling, leaving just pellets in the nest (pers. obs.). Other studies based on video monitoring have also showed this, and documented that the nestlings swallow microtine rodents whole (Tornberg & Reif 2007; Skouen 2012; Sonerud et al. 2014). Thrushes were often delivered to the nest without head and tarsi (pers. obs.), as this made the birds easier to ingest unassisted by the nestling. It is possible that decapitated birds were used as an alternative prey when microtine rodents were absent, so that the nestling could feed independently. The low number of delivered microtine rodents in my study may be the reason why my results differ from those of other studies.

Selection of prey

As the season progressed, the golden eagle pair delivered fewer mountain hares and more thrushes to the nest. According to optimal foraging theory, the profitability may be less for thrushes than for mountain hare, as the profitability per delivery to the nest is penalized for the cost of transport (MacArthur & Pianka 1966; Pulliam 1974; Stephens & Krebs 1986). Schweiger et al. (2015) found that small prey species delivered to the nest had larger relative energetic cost of transport, compared to relative energetic gain for prey consumption. Poor food conditions would drive the eagles to a wider diet, which may include small prey species to a greater extent (Schweiger et al. 2015). On the other hand, thrushes would make an easier target than large prey, and there may be a lower cost of capturing thrushes compared to larger prey species such as mountain hare. In my study the decrease in mountain hare in the diet throughout the season was apparently offset by an increase in the delivery of thrushes. This connection suggests that thrushes might have been an important prey to satisfy the dietary requirements of the nestling as it grew. A study in Japan (Takeuchi et al. 2006) made a similar finding, namely that snakes became a more important prey for the golden eagle nestlings later in the season, at the expense of the preferable Japanese hare (*Lepus brachyurus*). This may be explained by a shorter searching and handling time later in the season, as the temperature rise and the access to snakes' increased. A similar finding was made by Steen et al. (2011) on the Eurasian kestrel, where the predation on common lizards (*Zootoca vivipara*) increased with increasing ambient temperature. A higher abundance of thrushes later in the season, when the nestlings of the thrushes leave the nest, makes the golden eagles' hunt for thrushes easier. In addition, mountain hare may also be easier to catch earlier in the season, when the hare population consists of many juvenile individuals. The golden eagle would consequently most likely change its diet accordingly, from larger prey as hare, to small prey species, such as thrush.

The probability that a prey delivered to the nest was a mountain hare declined with increasing precipitation. This might be explained by a higher availability of small prey items, such as thrushes, when it rained (see below). Another explanation may be the effect of rain on the behaviour of other species, and on the raptors hunting behaviour (Hirons 1982). Golden eagles mainly find their prey by searching from air (Watson 2010). Days with high precipitation and poor weather conditions may increase searching time for mountain hare. Consequently, the proportion of thrushes in the diet may increase on days with high precipitation.

The probability that a prey delivered to the nest was a thrush increased with precipitation and nestling age. This may be explained by the foraging behaviour of thrushes. Thrushes prefer to forage during rain, for instance on earthworms (pers. obs), which are more exposed on the ground during rain, and therefore may be more exposed to thrushes. An explanation for increased deliveries of thrushes with increasing nestling age, could be that the nestling fed unassisted more often with increasing age. Therefore, the male should deliver prey items that the nestling could feed on without assistance from the female, which would lead to a better pay-off from the male's foraging effort (Sonerud et al. 2013). The nestling fed unassisted earlier on small prey items than larger ones, in accordance to findings of Sonerud et al. (2013). Directly deliveries to the nest is preferable for the male because it prevents the female from eating the prey herself (Sonerud et al. 2013). The male delivered more thrushes directly to nest than to the female, which corresponds with findings on the kestrel (Sonerud et al. 2013). Male kestrels delivered small prey items directly to the nestling, which made it possible for nestlings to feed unassisted. Larger prey, on the other hand, were delivered to the female, followed by assisted feeding to the nestling. Delivering items which is easier to ingest unassisted by the nestling, is preferable as it frees the female from feeding the nestling, and making both parents able to hunt at the same time (Sonerud et al. 2013). The amount of time the female supports the male with hunting would depend on prey type (Sonerud et al. 2014), and whether there is sufficient amount of prey available, in which case the female can rely on the male's hunting success (Sonerud et al. 2013).

I found that the male was more likely to deliver birds, as also found by Skouen (2012) and Dihle (2015). This could be explained by the higher abundance of birds, and newly fledged nestlings later in the season. Another explanation suggested by Sonerud et al. (2013) propose a new hypothesis on the selection of male and female body size in relation to diet, where the role symmetry increases as the diet changes from insects via reptiles and mammals to birds. As most raptors the golden eagle has reversed sexual size dimorphism, i.e. the male has smaller body size than the female. Sexual dimorphism is greatest between species that feed on agile prey such as birds (Newton 1979). The female need to allocate the food delivered by the male between herself and the nestling during the period when she feeds the nestling, and this may select for larger female body size (Sonerud et al. 2013; Sonerud et al. 2014). The male may respond to this with delivering more small prey items, which then selects for smaller male body size (Sonerud et al. 2013). This is in line with Newton (1979), who suggest that raptors have a selective advantage of being close to the size of its prey when hunting agile prey species. The male golden eagle may therefore deliver more small prey items later in the season, as an attempt to increase the nestlings fitness and then also his own fitness. However, the bird delivering the prey at the nest is not necessarily the bird that captured the prey (Sonerud et al. 2013).

Win-stay or win-shift hunting strategy

I found willow grouse to be a common prey, but the probability that a grouse was delivered short time after the last grouse delivery was low, and was not related to the previous prey delivered. This may be because of the relatively high body mass of grouse, and that the eagle parents have satisfied the nestling’s current need for food. Another explanation proposed by Skouen (2012) is that the hunting strategy is a choice made by the eagles, based on the prey species’ distribution. One hypothesis suggested by Sonerud (1985), is that extensive brood movements preformed by grouse species and waders, is a defence strategy against single-prey loaded, central place (CP) foraging raptors that use the win-stay search strategy. To explain this, Sonerud (1985) argued that a predator that are going to start a new hunt needs to make a decision at the start of the hunt. This decision is made based on three prey distribution patterns (Sonerud 1985). The predator may choose to 1) search at random, if the prey is randomly distributed, 2) postpone its return to the capture site, if the prey is uniformly distributed and temporary reduced after previous hunt, or 3) return rapidly to the capture site rather than searching at random if the prey has a clumped distribution (Sonerud 1985). This hypothesis assumes that the predator remembers the prey species’ location from the previous hunt, and that the next hunt will be based on the memory from earlier captures or discovery sites to find a new prey (Sonerud 1985; Mitchell & Lima 2002).

Roth & Lima (2007) found that sharp-shinned hawks (*Accipiter striatus*) hunted randomly to avoid antipredator behaviour among the prey species. The hawk visited areas inside their home range only a few times, and areas were revisited with an unpredictable return time, although the home range included several prey hotspots such as bird feeders (Roth & Lima 2007). The hawks' hunting behaviour may be effective in areas where the prey species is numerous with high vigilance. However, the hawks' attack success decreased if the attacks happened too often and were predictable (Roth & Lima 2007). Similarly, Redpath (1992), studied the interaction between hen harriers (*Circus cyaneus*) and grouse, and found no indication of a win-stay strategy. The explanation why golden eagles apparently did not hunt grouse with the win-stay hunting strategy is that the grouse start to move shortly after hatching (Sonerud 1985; Mitchell & Lima 2002). This supports that raptors should search at random (prey distribution patterns 1) to increase their success when hunting grouse. This behaviour is termed the win-shift hunting strategy, and was also observed in sharp-shinned hawks when hunting avian prey (Roth & Lima 2007).

There was a higher probability that the next prey delivered was a thrush if the last prey also was a thrush, and the probability of two thrushes to be delivered in "runs" decreased with time elapsed since the previous thrush was delivered. This is in accordance with the results presented by Skouen (2012) suggesting that the golden eagles' tactic when hunting thrushes is a win-stay strategy. Thrushes suits Sonerud's (1985) third prey distribution pattern, a clumped distribution. The best hunting strategy for an eagle that have captured a thrush at a site is then to rapidly revisit this site (Sonerud 1985; Mitchell & Lima 2002). An eagle's increased probability to recapture a thrush if it returned rapidly to the capture site (prey distribution patterns 3) is further supported by the breeding tactic of one of the common thrushes, the fieldfare, who often breed in colonies (Svensson et al. 2010). In general, the average size of each thrush brood is 4-6, and the young are often in close proximity to the nest the first weeks after fledging. In the nesting season, thrushes are confined to the nest, and therefore they may be unable to develop an evasive antipredator behaviour. This is in contrast to the prey of sharp-shinned hawk, because the thrushes have to take care of their nestlings on site.

In my study, win-stay and win-shift strategies are inferred based on prey deliveries at the nest, which is not ideal. In order to truly understand the golden eagles hunting strategy, studies that include GPS trackers, should be conducted. This may give more information about where and when the golden eagles hunt.

Biases and implications

I monitored only one golden eagle nest, so my results reflect only the diet during the nestling period. The diet of the golden eagle may vary considerably between individuals, habitats, seasons, years, and different parts of the world (Watson 2010). The results should therefore be interpreted cautiously, as the sample size was low (Bissonette 1999). Video monitoring do only record prey items delivered at the nest. Small prey items may be ingested immediately at the capture site (Sonerud 1989, 1992), thus the number of small prey species might be underestimated even by video monitoring at the nest. Nesting eagles may not predate on livestock, and therefore, video monitoring at the nest may be a insufficient method to reveal predation on livestock. Immature non-nesting golden eagles are more likely to be responsible for the potential predation on livestock (Watson 2010). Video monitoring at nests is cost-saving, and time-effective, compared to other methods (Steen 2009; Cox et al. 2012). High pixel-rate on the recording equipment makes it easier to define the delivered prey item to species, and motion sensors also reduce the time spent on determining prey deliveries (Steen 2009). However, the identification of prey items may be difficult under some conditions, and the identification may be incorrect due to human error. My study was conducted without major problems with the recording equipment, however there could be minor problems, and some prey deliveries to the nest may not have been recorded due to either technical issues or human errors.

Conclusion

Birds were the most common prey at the nest of one pair of golden eagle in Oppland County. A surprisingly large part of the birds was thrushes, which were the most important prey late in the season. Willow grouse were the second most important avian prey species, despite the estimated low population density in the area for the studied year. Mountain hare was the most important prey with respect to biomass, and especially early in the season. My study, as other studies based on video monitoring, has revealed a larger proportion of small prey species in the diet of the golden eagle, compared studies based on analysis of prey remains and pellets. Only one *Microtus* vole was delivered at the nest, as expected due to the crash of the microtine rodent populations in the region. My study is the third study conducted with video monitoring in Norway (and Europe), and none of these have registered any sheep or other ungulates delivered at the nest. This is in contrast to the main belief, as sheep is released on summer grazing during the golden eagle breeding season. The golden eagle nestling started to feed unassisted on birds earlier than on mammalian prey, in contrast to what found in other studies. This study supports the finding that the golden eagles' hunting strategy on willow grouse is win-shift, while the strategy on thrushes is win-stay. However, my study has only analysed the prey items delivered at one nest, and has hence a small sample size. To further give a good analysis of the golden eagles diet, and strengthen the statement that sheep and other livestock are not an important part of the golden eagle diet, more studies with video monitoring are needed. Studies should also be conducted in other regions, include all seasons, and consist of more golden eagle pairs. The eagle's change in diet during the season should be compared with frequent estimates of prey abundance. In addition, the use of GPS trackers on the breeding birds would give a better understanding of the golden eagles' habitat choice, and when and where they capture their prey.

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