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Diet, prey deliveries and prey handling of nesting golden eagles (*Aquila chrysaetos*) in Oppland county, Norway, as revealed by video monitoring of four nests throughout the nestling period

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Abstract

In this study I used video monitoring of nests throughout the nestling period to study diet, prey deliveries and prey handling of four breeding pairs of golden eagles (*Aquila chrysaetos*) in Oppland county, Norway. A total of 456 prey items were recorded delivered at the nests. In total, the following prey items were registered: 296 birds (64.9%), 135 mammals (29.6%), 3 reptiles (0.7%), 1 amphibian (0.2%) and 21 (4.6%) prey items that could not be identified to a prey group. The most common prey species by numbers were willow grouse (*Lagopus lagopus*) (25%) followed by thrushes (*Turdus* sp.) (16.3%) and mountain hare (*Lepus timidus*) (11.2%). In terms of biomass, mammals was the most important prey group and mountain hare the most important prey species (accounting for 41.8% of the total delivered net biomass). Parts from a total of four domestic sheep (*Ovis aries*) were recorded delivered at the nests, but it is unknown whether the sheep were found dead or killed by the eagles. There were differences in the diet between the nestling periods of 2018 and 2019. Microtine rodents accounted for 17.3% of the diet in 2018 which was a peak year for microtine rodents in the study area. In contrast, no microtine rodents were recorded delivered in 2019, which was a low year for microtine rodents. In 2019 the diet consisted of a total of 89.1% birds, compared to 56.2% in 2018. The probability that a prey item was decapitated prior to delivery at the nest increased significantly with increased gross prey mass and there was a trend that the probability decreased as the nestling became older. The female was the only parent participating in the feeding of the nestlings and did so in 57% of the cases. On average, the nestlings started to feed unassisted when they were 44 days old. When approximately 50 days old it became more likely that the nestling fed unassisted on the smallest prey items (65 days old for the larger prey items). The male delivered most of the prey items to the nests (63%). The male delivered 77% of the birds while the female delivered 69% of the mammals, including 90% of the microtine rodents. The female contributed significantly more in the hunting as the nestlings became older. My study supports the reputation of the golden eagle to be an opportunistic hunter. I found that a minimum of 34 different prey species from four different taxonomic classes (mammals, birds, reptiles and amphibians) were delivered to the nests. However, the golden eagle diet seems to be a result of variations in prey availability (in time and space) within the eagle's territories.

Sammendrag

I denne oppgaven har jeg brukt videoovervåking gjennom perioden ungene var i reiret, til å studere diett, byttedyrleveringer og byttedyrhåndtering hos fire hekkende par kongeørn (*Aquila chrysaetos*) i Oppland fylke i Norge. Totalt ble 456 byttedyr registrert levert på reirene. Av disse ble det registrert 296 fugler (64,9 %), 135 pattedyr (29,6 %), 3 reptiler (0,7 %), 1 amfibium (0,2 %) og 21 (4,6 %) byttedyr som ikke lot seg identifisere til en byttedyrgruppe. Det mest tallrike byttedyret var lirype (*Lagopus lagopus*) (25 %) etterfulgt av troster (*Turdus* sp.) (16,3 %) og hare (*Lepus timidus*) (11,2 %). Basert på vekt var pattedyr den viktigste byttedyrgruppen og hare den viktigste byttedyrarten (41,8 % av den totale netto vekten levert på reirene). Deler fra totalt fire sauer (*Ovis aries*) ble levert på reirene, men det er ukjent hvorvidt ørnene fant sauene døde eller tok livet av dem selv. Det var noen forskjeller i dietten mellom sesongene 2018 og 2019. Smågnagere sto for 17,3 % av dietten i 2018 som var et toppår for smågnagere i studieområdet. Derimot ble det i 2019 ikke registrert noen smågnagere levert på reiret i det som var et bunnår for smågnagere i studieområdet. I 2019 besto dietten av totalt 89,1 % fugler sammenlignet med 56,2 % i 2018. Sannsynligheten for at et bytte var dekapitert før levering på reiret økte signifikant med økt brutto byttedyrvekt og det var en klar trend at sannsynligheten minket etter som ungen ble eldre. Hunnen var den eneste av foreldrene som hjalp ungene med å spise, og bisto i 57 % av situasjonene. I gjennomsnitt startet ungene å spise alene etter 44 dager. Etter om lag 50 dager for de mindre byttedyrene, og etter om lag 65 dager for de større byttedyrene, ble det mer sannsynlig at ungene spiste på egenhånd enn at de ble hjulpet av hunnen. Hannen leverte mesteparten av byttedyrene på reiret (63 %). Hannen leverte 77 % av fuglene mens hunnen leverte 69 % av pattedyrene inkludert 90 % av smågnagerne. Hunnen deltok mer i jakten på mat etter hvert som ungene ble eldre. Studiet bekrefter kongeørnas rykte som opportunistisk jeger. Totalt registrerte jeg minst 34 forskjellige arter av byttedyr fordelt på fire taksonomiske klasser (pattedyr, fugler, reptiler og amfibier) levert på reirene. Dietten ser imidlertid ut til å variere basert på byttedyrenes tilgjengelighet (i tid og rom), innenfor ørnenes territorier.

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Introduction

Species within an ecosystem are connected in a complex network of predator-prey interactions. Chares Darwin called this an "entangled bank", but today *food web* is a more common term (Darwin 1859; Zanden et al. 2016). The top predators in these food webs are called apex predators. They influence whole ecosystems by limiting prey populations and controlling smaller predator populations (Wallach et al. 2015). Knowledge about the diet of top predators is key to understand ecosystem dynamics and what cascading effects top predators can have on the rest of the food chain (Zanden et al., 2016).

The golden eagle (*Aquila chrysaetos*) is a typical predator on top of the food chain. It is a widespread raptor found across the Northern Hemisphere including the Palearctic and Nearctic regions, with an isolated sub-Saharan population in Ethiopia. Golden eagles are known to be opportunistic hunters able to capture down a range of different prey species (Kochert et al. 2020). As a result, golden eagles have adapted to a wide range of habitats across their distribution area, ranging from mountains, coastal islands, boreal woodland and even deserts. Typically, golden eagles are found in habitats with open landscapes suitable for hunting with cliffs or trees for nesting, often in areas where the human population is sparse (Watson 2010).

In Norway, the golden eagle is regarded as a typical mountain bird, but it is also found along the coast, especially in the northern parts of the country (Gjershaug 1994). It usually nests towards the upper parts of the boreal forest and hunt both above and below the tree line in habitats including alpine areas, heathland and open forests (Watson 2010). In Norway, the golden eagle has been protected by law since 1968. Prior to this, the Norwegian population of golden eagle had decreased dramatically due to hunting and killing of eagles. However, after the protection, the population has slowly increased, and the population seems to have stabilized since year 2000 (Hagen 1952; Dahl 2015).

Between 2010 and 2014, the breeding population of golden eagles in Norway was estimated to number 963 breeding pairs. A similar number of non-territorial birds was estimated, which means the total population of golden eagles in Norway number approximately 3850 individuals, which is a significant proportion of the European population (Dahl 2015). In 2018, the population of golden eagles in Oppland county was estimated to number 55-65 breeding pairs (Kistefos Skogtjenester, unpubl. data). Globally, the golden eagle is not considered threatened by the IUCN. The global population is estimated to number approximately 300,000 individuals, which equates to 200,000 mature individuals (BirdLife International 2016).

The golden eagle is a well-studied raptor and its diet has been examined in many parts of its distribution range (Hagen 1952; Nyström et al. 2006; Watson 2010; Harrison et al. 2019). More than 400 vertebrate species have been recorded as prey, showing that the golden eagle is an opportunistic and skilled hunter capable to adapt to many different environments and hunting a range of different prey types (Watson 2010). Prey selection differs widely across its range and is largely determined by the local availability and abundance of prey species (Watson 2010). Anyway, most of the diet usually consists of medium-sized mammals like rodents, rabbits and hares and birds ranging in size from small passerines (*Passeriformes* sp.) to cranes (*Gruidae* sp.). The most common birds are Galliformes such as grouse and ptarmigans, for example the willow grouse (*Lagopus lagopus*). Golden eagles even prey on reptiles and amphibians, but much less frequently. Carrion can also be important, especially during winter (Watson 2010; Kochert et al. 2020).

Multiple methods have been used to acquire knowledge about the diet of golden eagles across its range. Traditionally, most studies examining the diet were based on indirect methods such as analyses of prey remains and regurgitated food pellets collected from nests. Other traditional methods include direct observation of the nest from a distance using binoculars or analysis of stomach content of dead birds (Watson 2010). These traditional methods all have their limitations and with new technology and equipment, more modern methods are now available. In this study, I used video monitoring of nests to study the golden eagle throughout the nestling period. Video monitoring makes it possible to study the eagles around the clock with minimal disturbance. At the same time, it is a cost-efficient method with the potential of collecting much data with a relative low cost and effort. In addition to diet studies, video monitoring of nests can reveal much interesting information. For example, it is possible to record hatching and fledging dates, competition between nestlings, parental roles and delivery rates. To the best of my knowledge, video monitoring has been used in three previous studies of golden eagle nests in Norway (Skouen 2012; Dihle 2015; Nygård 2015).

Some studies have shown that ungulates are part of the diet of golden eagles in some parts of its range (Sulkava et al. 1999; Johnsen et al. 2007; Nyström 2006; Watson 2010). Ungulates found in the diet include domestic livestock, mostly lambs of domestic sheep (*Ovis aries*) and fawns of domestic reindeer (*Rangifer tarandus*). Each year the Norwegian government pays compensation to livestock farmers for lost income due to predation from predators, including the golden eagle (Rovbase 2020). However, there are some controversy regarding how important golden eagles are as a predator on domestic livestock.

To obtain good management and conservation strategies for the golden eagle, and thus a stable population also in the future, knowledge about which prey species that are most important in their diet is required (Watson 2010). Therefore, I used video monitoring to study four occupied golden eagle nests in a mountainous region in southern Norway during the nestling period. The aims of my study were, to 1) determine the diet of the golden eagles during the nestling period, and reveal the most important prey species, including whether domestic sheep were part of their diet, 2) compare the diet between the nestling periods of 2018 and 2019, where 2018 was a peak year and 2019 a low year for microtine rodents in the study area, and 3) investigate parental roles, prey handling prior to and after delivery at the nest, and patterns of the probability of when the main prey groups and species were delivered at the nests.

Methods

Study area

This study was conducted in Oppland county (since 2020 part of Innlandet county) in southern Norway at 61°20′- 61°45′ N; 9°50` - 9°95` E (exact position is confidential). The field work was conducted during the nestling period of the golden eagles (from mid-May until the start of August) in 2018 and 2019. The study area was located in the upper altitudinal limit of the boreal woodland in Gausdal and Sør-Fron municipalities. The nests were all located in cliffs at about 800-900 m above sea level, right below the tree line. The forests surrounding the nests were dominated by Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) intermixed with birch (*Betula* sp.). The nests were also close to open alpine areas with scattered areas of bogs and lakes. There were also farms with farmland in the area, many of which were mainly used during summer as grazing land for domestic sheep and cattle.

Video monitoring

In both 2018 and 2019 cameras were installed at six known golden eagle nests in the area. The nests were situated in an area of about 400 km^2 with about 14 km between each nest. Breeding pairs of golden eagles are known to build several nests within their territory where the nests are used alternately over the years. Usually a pair have 2-3 alternative nests, where one is used most frequently. However, pairs with up to eight different nests are known (Kochert et al. 2020). Therefore, one need to install cameras on multiple nests in order to have a reasonable chance of breeding in one of the nests with camera installed. At the same time golden eagles can be sensitive to humans, and in order to minimize disturbance, installation of cameras was done prior to the breeding season (during autumn) when the eagles did not use the nests. In mid-May 2019 we checked the status at all six nests to determine whether the eagles were breeding or not. Breeding was confirmed at only one of the six nests and video monitoring was started on May 16th. That day there was one nestling present in the nest, and it was estimated to be approximately three days old.

My original plan was to limit this study to data collected from the nestling period of 2019. However, since there was only one breeding pair of golden eagles at the nests where we had cameras mounted, I got to use unanalyzed recordings collected from the nestling period of 2018. In 2018, golden eagles were breeding at three of the six nests with cameras. There was one nestling in one of the nests and two nestlings in the other two but at one of these the youngest sibling died due to siblicide when it was approximately 26 days old.

Once breeding was confirmed at a nest, usually shortly after hatching, the video cameras were activated. Then the cameras were active throughout the whole nestling period until the nestling(s) left the nest and didn't return - sometime in late July or early August.

Figure 1. Still pictures taken from the video recordings from two of the golden eagle nests studied. The picture on the left shows the female (in the middle) with a Norway lemming (*Lemmus lemmus*) in its beak and the two nestlings (in the front). The picture on the right shows the female (on the left) assisting the nestling (on the right) with feeding on a Eurasian badger (*Meles meles*).

The method used for video monitoring the nests is the same as described by Steen (2009). The cameras used were CCD (charged-coupled device) cameras equipped with a wide-angle lens. The cameras had IR light allowing recording also at night. Prior to installing, the side of the cameras were painted with camouflage colors in order to blend in with the environment as much as possible. Depending on the nest sites, cameras were either mounted on the stem of a tree or in the rockface close to the nest. The position of the camera, and the wide-angle lens, allowed view of the whole nest in addition to some of the surrounding area. This setup offered good views of both prey deliveries and prey handling. The cameras were connected to a mini digital video recorder (mini DVR) by a 100 m long video cable stretched from the camera at the nest to a base station placed on the ground 50-100 m away from the nest. The mini DVR and camera were powered by a 12 V battery. In addition, a solar cell panel was connected to the battery to charge it, so it would last longer. The mini DVR and the battery were placed in waterproof boxes and covered by a tarpaulin. This setup allowed visits to the base station for collecting recordings and checking battery status with minimal disturbance to the eagles.

The mini DVR stored the recording data on 32 GB SD-cards. The SD-cards had to be changed approximately once every week. Two different SD-cards were used to ensure safe transforming of data and continuous recordings. The data from the SD-cards were transformed to a computer using a SD-card reader and stored on a hard drive disk for backup. A sample of the recording were checked to see that everything worked as planned. I visited the base station approximately once a week and the whole procedure took less than 15 minutes.

To limit the amount of irrelevant video recordings, I used a motion sensor detecting any movements close to the edge of the nest, e.g. when one of the parent eagles arrived at the nest with a prey. When the camera was triggered it recorded 5 s before the movement and kept recording until there no longer was movement. The sensitivity of the motion sensor was set to high so it would catch every prey delivery and prey handling at the nest. The resolution was 704 x 560 lines, and the frame rate was 25 pictures per s. The date and time of day was always recorded when the camera was filming so this could be used in analysis of prey deliveries and activity patterns.

In total, the cameras were active for approximately 4000 hours at the four golden eagle nests. During this period approximately 75,000 video clips were recorded. However, due to different technical problems, there were periods (from a few hours to several days) when the cameras were not active. Therefore, the results and conclusions are based on the prey deliveries I actually recorded, and it does not necessarily show the total picture.

Analysis of video recordings

After all the data were collected in the field, I started sorting out recordings of interest (containing prey deliveries and prey handling) in order to identify the different prey items to the lowest taxonomic level possible. All interesting recordings were then studied on a large screen, sometimes frame by frame, together with my supervisor. For each prey item delivered I also registered date and time of day, the age of the nestling, the sex of the delivering parent, whether the prey was decapitated, eaten at or plucked (if bird), and whether the nestling was fed by the female or fed unassisted.

In addition, both gross and net body mass were estimated, meaning the weight of the prey when it was caught by the eagle and the weight of the prey when it was delivered at the nest. For prey items that remained unidentified I did not get any data on weight because this would be hard to estimate. Information about the weight of different types of prey were collected from literature (Cramp & Simmons 1977; Cramp & Simmons 1980; Cramp & Simmons 1983; Cramp 1985; Cramp 1988; Frislid & Semb-Johansson 1990; Cramp 1992; Cramp & Perrins 1993; Cramp & Perrins 1994a; Cramp & Perrins 1994b). When estimating the net body mass of decapitated birds, I excluded 12.9% of the total body mass (Sonerud et al. 2014). When estimating the weight of incomplete mammal prey items like parts of a mountain hare (*Lepus timidus*), I excluded 20% of the total estimated weight if it was decapitated, another 10% if the front legs were missing and another 20% if the front part was also missing. A common example could be when the back part of a mountain hare was brought to the nest, I then excluded 50% of the total body mass when calculating the net body mass. The gross body mass for domestic sheep and European roe deer were not estimated because the eagles only brought in smaller portions of these preys and it would have been difficult to determine gross weight with accuracy.

Hereafter, willow grouse refer to *Lagopus* sp., either willow grouse or rock ptarmigan (*Lagopus muta*). All the prey items of this category that were possible to identify to species level were willow grouse, but it cannot be ruled out that there were also some rock ptarmigans in between the much more common willow grouse.

Data on temperature and precipitation for the time of each prey delivery were obtained from Skåbu meteorological station (Yr 2020). Here, temperature and precipitation were logged each hour throughout the day. The ambient temperature in the study area during the study period ranged from -3.4°C to a maximum of 26.7°C. Total precipitation throughout the nestling period (here defined as from 15th of May until 31th of July) was 76.3 mm in 2018 (0.7 mm in May, 21.1 mm in June and 54.5 mm in July, respectively) and 115.4 mm in 2019 (67.3 mm in May, 7.8 mm in June and 40.3 mm in July, respectively). Generally, both summers were dominated by dry weather with periods of very hot temperatures compared to previous years (Yr 2020).

Prey availability

Each year, the local property management, *Gausdal fjellstyre*, collects data on the density of willow grouse within the study area. Their data estimated a density of 12.9 willow grouse per km^2 in 2018 and 12.0 willow grouse per km^2 in 2019. Compared to the previous three years before 2018, the willow grouse population in the study area had increased (Hønsefuglportalen 2020).

Hunting bag data collected from Statistics Norway (Statistisk sentralbyrå) showed that 10 050 willow grouse and 3650 rock ptarmigans were shot in Oppland county during the hunting season 2018/19. For the season 2017/18, the respective numbers were 7 700 willow grouse and 3650 rock ptarmigans shot. The total number of willow grouse and rock ptarmigans shot during the 2017/18 and 2018/19 seasons, were higher than the two previous ones (SSB 2020).

Regarding microtine rodents, 2018 was a peak year in the study area. This included Norway lemming and *Microtus* voles in the mountains of Southern Norway. On the other hand, 2019 was a low year for microtine rodents after the population crashed between the seasons (G. A. Sonerud, pers. comm.).

The number of mountain hares shot in Oppland county during the hunting season was 2150 in 2017/18 and 2640 in 2018/19. In comparison, the average number of mountain hares shot during the previous five hunting season prior to the 2017/18 season was 2294 (SSB 2020). This indicates that the mountain hare population was higher than average in 2018.

Within the territories of the studied golden eagles, there are several farms with domestic sheep that are released to summer pastures in the start of June (pers. obs.). There are also domestic reindeer in some parts of the study area, at least in the western part, and reindeer fawns can be potential prey for the golden eagles.

Statistical analysis

The statistical analysis was performed in RStudio version 3.6.2 (R Core Team 2019) and JMP® (SAS Institute). Standard criterion of statistical significance was set to $\alpha = 0.05$ and residuals were checked for normality. In order to find the most fitted models, I selected the model with the lowest Akaike's information (AIC) after testing reasonable ecological variables against each other and then I selected the model with the lowest AIC value (Akaike 1974). Where the AIC value was approximately the same, I selected the model with the lowest number of variables. The selected model was then examined further. The construction of figures was done using RStudio (package 'ggplot'), JMP®, and Sigmaplot (Systat Software, Inc). Spreadsheet in Microsoft Excel for Office 365 (version 1908) was used for registering and organizing the data and for some of the simpler analysis.

I used contingency analysis to test the relationship between main prey group (bird or mammal) and delivering parent (male or female), and between prey group (mountain hare, willow grouse, microtine rodents, other birds or other mammals) and year (2018 and 2019).

To analyze diel activity and the probability of prey deliveries in relation to time of day, the day was divided into 24 hour-blocks and this was set to x in the model. The response variable was the probability of a prey item being delivered in a certain hour block. The response variable had two outcomes per hour-block: "no prey delivery" or "prey delivery". Then we modelled using logistic regression with a binomial distribution. The random effect was a correction for the nest ID, since I studied four different nests. The explanatory variable was time of the day. I used cosine curve fitting (cosinor) method since time of the day oscillate in 24-h cycles (Pita et al. 2011). The models are shown in table 2, for more details see Steen and Barmoen (2017).

Each model fit (M1–M3) was evaluated by comparing the AICc values with the model that included only the intercept (M0). Then the model fits were ranked according to their AICc values, with the lowest AICc value being considered the "most fitted". We selected the most parsimonious model with as few predictor variables as possible. The fitted curve from the best were compared with the midline estimating statistic of rhythm (MESOR), which expresses mean expected delivering rate when deliveries are random. When the confidence interval was higher than the MESOR, the delivery rate was higher than randomly expected and defined as significant.

I performed generalized linear mixed models to test for effects on the following response variables: the probability whether a prey item was decapitated prior to delivery, the probability of the nestling fed unassisted and the probability that the delivering parent was the female rather than the male. Explanatory variables on the probability of decapitation prior to delivery were nestling age and gross prey body mass. For the probability of the nestling feeding unassisted, the explanatory variables were nestling age and net prey body mass. For the probability of the female being the delivering se rather than the male the explanatory variables were nestling age and gross prey body mass. In all tests mentioned above the explanatory variables were tested separately and together, and nest ID was included as a random effect.

Results

Prey delivered at the golden eagle nests

A total of 456 prey items were recorded delivered at the four golden eagle nests that were monitored during the study period. The diet consisted of 296 birds (64.8%), 135 mammals (29.5%), 3 reptiles (0.6%), 1 amphibian (0.2%) and 21 (4.6%) prey items that could not be identified to a prey group (Table 1). The main prey by number was willow grouse which accounted for 25.0% of all items delivered. Thrushes were also numerous as prey and this group was the second largest prey group with 16.3% of all prey items. Mountain hare was the most numerous mammal delivered at the nests and accounted for 11.2% of all recorded prey items making it the third most important prey group by numbers. Mountain hare was also the most important prey species by biomass, accounting for 41.8% of delivered net prey mass. The second most important prey by mass was willow grouse accounting for 27.6%. Norway lemming and *Microtus* sp. made up a relatively large amount by numbers, with 8.1% and 3.1%, respectively, but of the total net prey mass delivered at the nests they made up only 0.9% and 0.4%, respectively (Table 1). The mean gross prey mass of all preys delivered (where it was possible to estimate) was 737 g. The mean net prey mass delivered at the nests was 532 g.

Domestic sheep as prey

Parts from a total of four domestic sheep were delivered at three of the four nests. Domestic sheep accounted for 0.9% of the total number of prey items and 2.6% of total net mass delivered at the nests (Table 1). The dates the parts of sheep were delivered at the nests were the 6th, 17th and 28th of June in 2018 and 20th of July in 2019. At one of the nests the eagles brought parts of sheep to the nest six times. There were probably multiple parts from no more than two individual sheep because of the short time in between deliveries and the size and color of the legs brought to the nest. The remains were from one black and one white colored sheep brought to this nest. In the other two nests with sheep there was only one occasion with sheep delivered and, on both occasions, there was a white colored sheep leg with some extra meat attached.

A total of minimum 34 different species from four different taxonomic classes (mammals, birds, reptiles and amphibians) were recorded delivered as prey at the nests. Except those mentioned above, most of these accounted for only a small proportion of the diet both by numbers and mass, but they demonstrate the great variety in the golden eagle's diet.

Table 1. Prey delivered at four golden eagle nests in Oppland county, Norway, as revealed by video monitoring during the nestling period. Numbers are given as total prey number with relative contribution per species (%), average estimated gross and net body mass per prey and for all prey and % of estimated gross and net body mass in the diet.

Prey species	Prey number		Gross body mass (g)			Net body mass (g)		
	N	%	Per prey	All prey	%	Per prey	All prey	%
Willow grouse / Rock ptarmigan (*Lagopus* sp.)	114	25.0	500	57000	21.4	471[1]	53736	27.6
Black grouse (*Tetrao tetrix*)	5	1.1	1060[3]	5300	2.0	1013[2]	5068	2.6
Western capercaillie (*Tetrao urogallus*)	4	0.9	2500[5]	10000	3.8	875[4]	3500	1.8
Black-throated diver (*Gavia arctica*)	1	0.2	200	200	0.1	200	200	0.1
Canada goose (*Branta canadensis*)	1	0.2	200	200	0.1	200	200	0.1
Common teal (*Anas crecca*)	1	0.2	300	300	0.1	300	300	0.2
Common goldeneye (*Bucephala clangula*)	1	0.2	700	700	0.3	700	700	0.4
Common crane (*Grus grus*)	4	0.9	2675[7]	10700	4.0	425[6]	1700	0.9
Eurasian woodcock (*Scolopax rusticola*)	2	0.4	300	600	0.2	300	600	0.3
Whimbrel (*Numenius phaeopus*)	4	0.9	400	1600	0.6	374[8]	1496	0.8
Common greenshank (*Tringa nebularia*)	4	0.9	200	800	0.3	200	800	0.4
Wader indet. (*Scolopacidae* sp.)	2	0.4	200	400	0.2	200	400	0.2
Northern hawk owl (*Surnia ulula*)	2	0.4	300	600	0.2	300	600	0.3
Short-eared owl (*Asio flammeus*)	2	0.4	380	760	0.3	380	760	0.4
Three-toed woodpecker (*Picoides tridactylus*)	1	0.2	65	65	0.02	65	65	0.02
Common raven (*Corvus corax*)	5	1.1	1200	6000	2.3	1107[9]	5535	2.8
Hooded crow (*Corvus cornix*)	3	0.7	500	1500	0.6	479[10]	1436	0.7
Fieldfare (*Turdus pilaris*)	13	2.9	100	1300	0.5	100	1300	0.7
Redwing (*Turdus iliacus*)	1	0.2	70	70	0.03	70	70	0.03
Thrush indet. (*Turdus* sp.)	62	13.6	100	6200	2.3	98[11]	6122	3.1
Passerine indet. (*Passeriformes* sp.)	2	0.4	20	40	0.02	20	40	0.02
Unidentified bird	62	13.6	-	-	-	-	-	-
Total bird	*296*	*64,8*	*11970*	*104335*	*39.37*	*7877*	*84628*	*43.47*
Mountain hare (*Lepus timidus*)	51	11.2	2588	132000	49.6	1600[12]	81450	41.8
Red fox (*Vulpes vulpes*)	3	0.7	3000[14]	9000	3.4	2000[13]	6000	3.1
Red squirrel (*Sciurus vulgaris*)	2	0.4	300	600	0.2	300	600	0.3
Mink (*Mustela vison*)	2	0.4	600	1200	0.5	600	1200	0.6
Least weasel (*Mustela nivalis*)	1	0.2	40	40	0.0	40	40	0.02
Stoat (*Mustela erminea*)	6	1.3	166[15]	1000	0.4	166[15]	1000	0.5
Pine marten (*Martes martes*)	5	1.1	1200	6000	2.3	1080[16]	5400	2.8
Badger (*Meles meles*)	1	0.2	5000	5000	1.9	4000	4000	2.1
Domestic cat (*Felis catus*)	1	0.2	4000	4000	1.5	2000	2000	1.0
European roe deer (*Capreolus capreolus*)	1	0.2	-	-	-	1000	1000	0.5
Domestic sheep (*Ovis aries*)	4	0.9	-	-	-	1250[17]	5000	2.6
Norway lemming (*Lemmus lemmus*)	37	8.1	50	1850	0.7	50	1850	0.9
Field vole / Root vole (*Microtus* sp.)	14	3.1	50	700	0.26	50	700	0.4
Unidentified mammal	7	1.5	-	-	-	-	-	-
Total mammal	*135*	*29.5*	*16994*	*161390*	*60.76*	*14136*	*110240*	*56.62*
European adder (*Vipera berus*)	1	0.2	300	300	0.11	300	300	0.2
Viviparous lizard (*Zootoca vivipara*)	2	0.4	10	20	0.01	10	20	0.01
Common frog (*Rana temporaria*)	1	0.2	20	20	0.01	20	20	0.01
Unidentified prey	21	4.6	-	-	-	-	-	-
Total	**456**	**99.7**	-	**266065**	**100.3**	-	**195018**	**100.3**

[1] Mean estimate, variation 436-500 g
[2] Mean estimate, variation 784-1300 g
[3] Mean estimate, variation 900-1300 g
[4] Mean estimate, variation 500-1000 g
[5] Mean estimate, variation 2000-4000 g
[6] Mean estimate, variation 200-500 g
[7] Mean estimate, variation 200-5000 g
[8] Mean estimate, variation 348-400 g
[9] Mean estimate, variation 1045-1200 g
[10] Mean estimate, variation 436-500 g
[11] Mean estimate, variation 87-100 g
[12] Mean estimate, variation 500-3000 g
[13] Mean estimate, variation 1000-3000 g
[14] Mean estimate, variation 2000-4000 g
[15] Mean estimate, variation 100-200 g
[16] Mean estimate, variation 600-1200 g
[17] Mean estimate, variation 500-2000 g

Delivery patterns for the main prey types

Prey deliveries were recorded in 22 out of the 24 hours of the day. The earliest prey delivery was recorded 03:48 and the latest was recorded 00:19. The delivery rate was significantly higher than randomly expected from around 08 hours until around 19 hours and significantly lower than randomly expected from around 21 hours until 06 hours. There was a peak in prey deliveries late in the morning from around 08 hours until 11 hours. After this the activity level dropped again before there was a new peak in activity in the early evening from around 17 hours until 19 hours. After this the activity dropped again and remained low until the next morning (Figure 2).

For details regarding model selection when analyzing prey deliveries in relation to the time of day see "Statistical analyzes" under the methods chapter. The results of the model selection based on AIC analysis is shown in Table 2. Based on Akaike weights, model 3 was likely to be the best fitted model and was selected to be tested further (Table 2).

Table 2. Output of the model selection based on AIC analysis for models of factors affecting the probability of prey delivery at the golden eagle nest in relation to the time of the day, with AIC values together with ΔAIC and AIC-weight.

Model	Variables	K	AIC	ΔAIC	AIC-weight
3	Prey delivery + I(cos(2*pi*Hour/24)) + I(sin(2*pi*Hour/24)) + I(cos(2*2*pi*Hour/24)) + I(sin(2*2*pi*Hour/24)) + ID	6	2131.71	0.00	0.69
4	Prey delivery + I(cos(2*pi*Hour/24)) + I(sin(2*pi*Hour/24)) + I(cos(2*2*pi*Hour/24)) + I(sin(2*2*pi*Hour/24)) + I(cos(3*2*pi*Hour/24)) + I(sin(3*2*pi*Hour/24)) + ID	8	2133.31	0.31	0.31
2	Prey delivery + I(cos(2*pi*Hour/24)) + I(sin(2*pi*Hour/24)) + ID	4	2175.11	43.40	0.00
1	Prey delivery + ID	2	2318.93	187.22	0.00

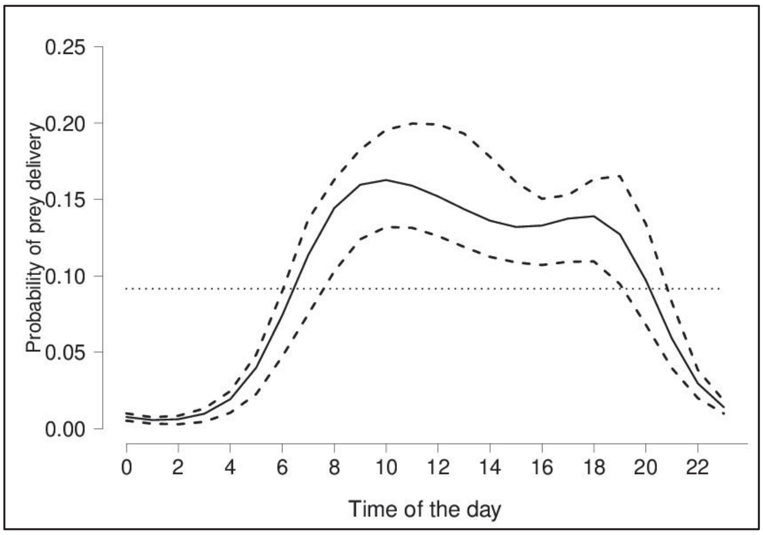

Figure 2. The probability of prey delivery at a golden eagle nest per hour block throughout the day, represented by the black solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal dashed line represents the midline estimating statistic of rhythm (MESOR).

Birds were delivered at the nests throughout the whole day and there was a significantly higher delivery rate than randomly expected from about 09 hours until about 18 hours. For mammals there was a significantly higher delivery rate than randomly expected from about 08 hours until about 12 hours and significantly lower than randomly expected from about 21 hours until about 06 hours (Figure 3).

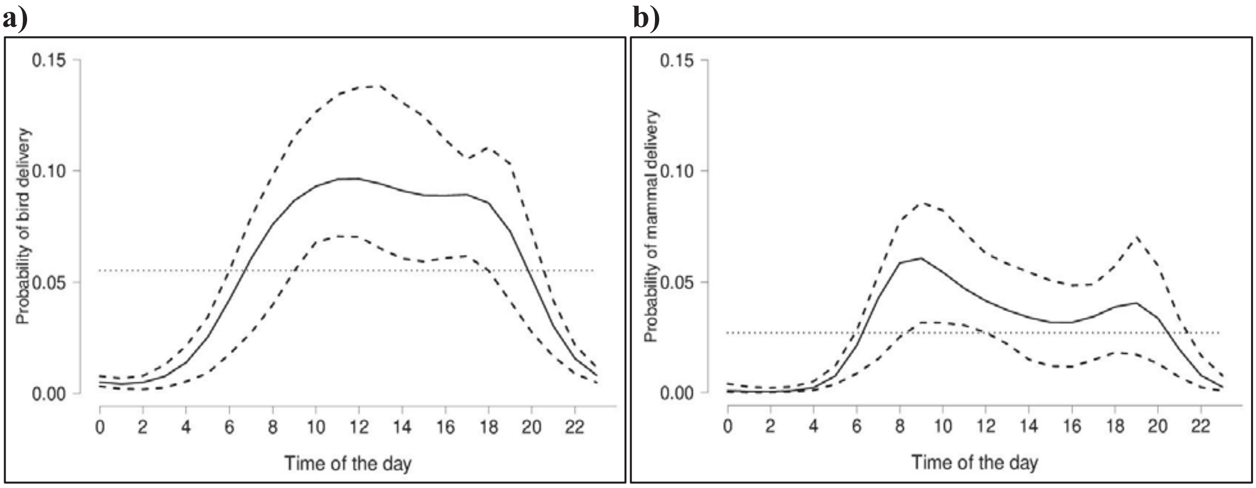

Figure 3. The probability of a bird (**a**) and mammal (**b**) delivered at a golden eagle nest per hour block throughout the day, represented by the black solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal dashed line represents the midline estimating statistic of rhythm (MESOR).

Willow grouse was the most numerous prey species and were delivered at the nests throughout the whole day from early morning until the evening (Figure 4). However, the delivery rate was not higher than randomly expected for any hours, while it was significantly lower than randomly expected from about 21 hours until about 04 hours.

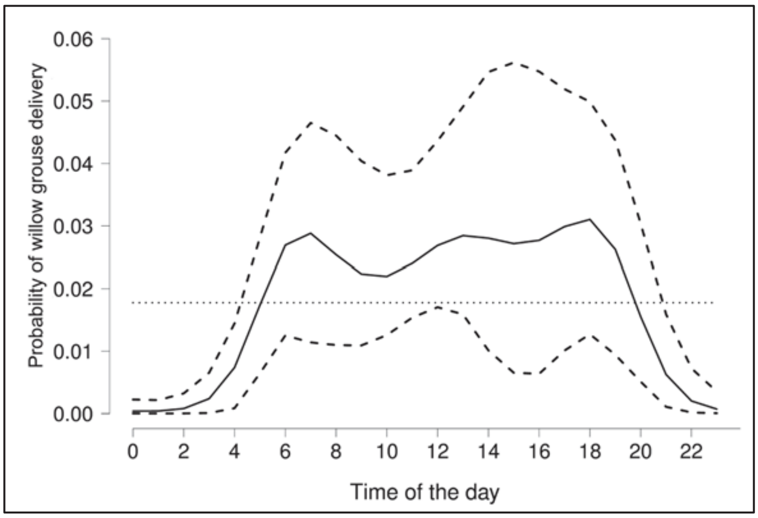

Figure 4. The probability that a willow grouse was delivered at the golden eagle nest per hour block throughout the day, represented by the black solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal dashed line represents the midline estimating statistic of rhythm (MESOR).

Mountain hare was the most common mammalian prey species delivered at the nests. Mountain hare was delivered significantly more often than randomly expected from about 07 hours until around 12 hours and significantly less often than randomly expected from around 22 hours until around 05 hours (Figure 5).

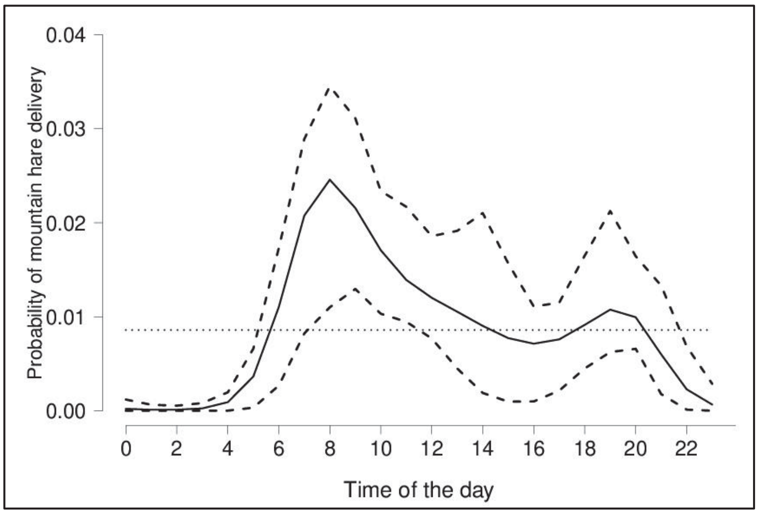

Figure 5. The probability that a mountain hare was delivered at the golden eagle nest throughout the day, represented by the black solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines. The grey horizontal dashed line represents the midline estimating statistic of rhythm (MESOR).

Differences in the diet between the nestling periods of 2018 and 2019

There were multiple differences in the proportions of the different main prey groups in the diet between the nestling periods of 2018 and 2019. The most significant difference was that microtine rodents was the second most numerous prey group in 2018, but completely absent in 2019. Also, birds accounted for 56.2% of the diet in 2018, while in 2019 birds accounted for as much as 89.1% of the diet. The proportion of mammals in the diet was much higher in 2018 with 42.6% compared to only 10.3% in 2019 (Figure 6).

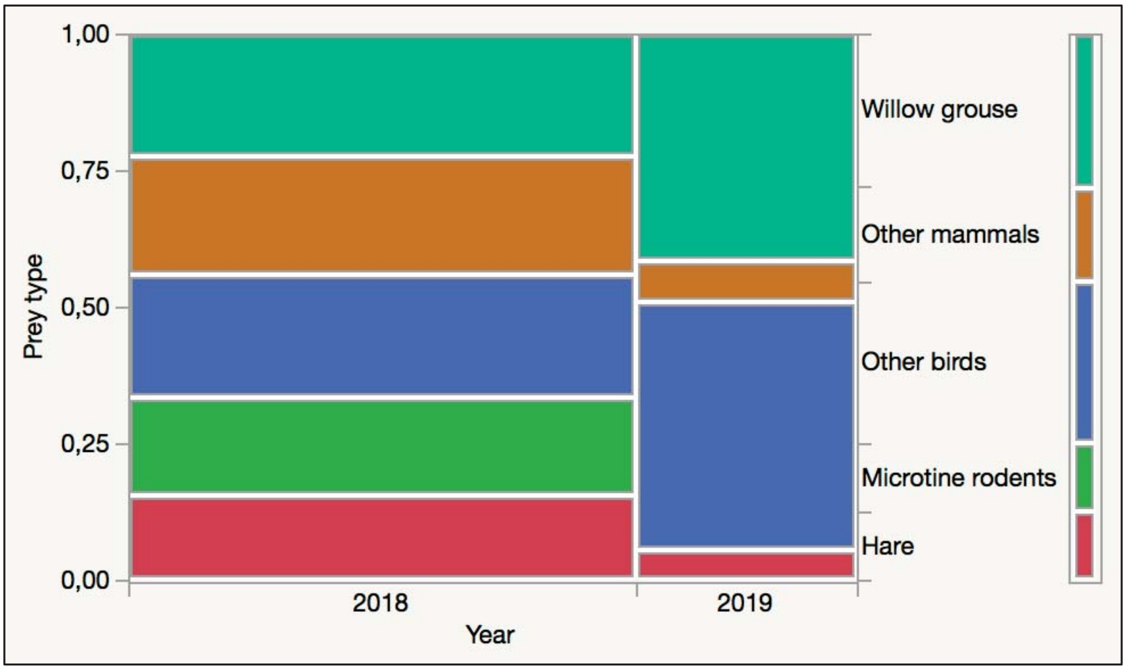

Figure 6. The distribution of prey type (willow grouse, microtine rodents, mountain hare and other birds and mammals) on year (2018 and 2019) delivered at four golden eagle nests. Whole model: N=406, $\chi^2 = 65.37$, df= 4, $p < 0.0001$.

Willow grouse was the most important prey species in both 2018 and 2019. However, it accounted for a bigger proportion of the diet in 2019 when it accounted for 32.7% compared to 22.6% in 2018 (Figure 7).

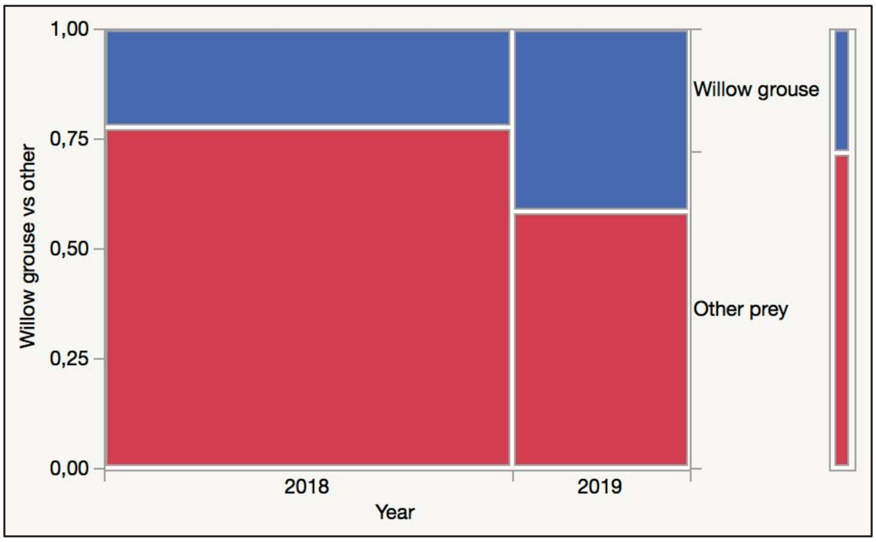

Figure 7. The distribution of prey type (willow grouse and other prey) on year (2018 and 2019) delivered at four golden eagle nests. Whole model: N=406, $\chi^2 = 15.65$, df= 1, $p < 0.0001$.

Microtine rodents, including Norway lemming and *Microtus* sp., accounted for 17,3% of the diet in 2018. In contrast, no microtine rodents were recorded delivered at the nest in 2019 (Figure 8).

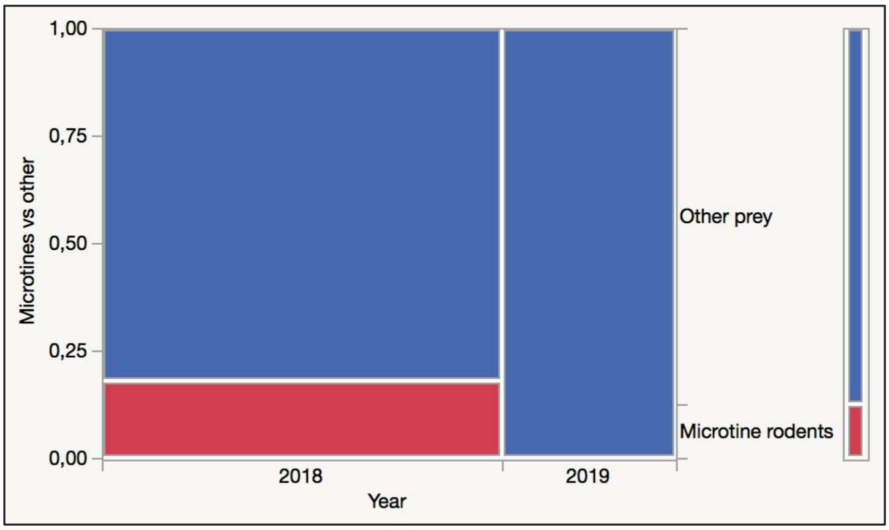

Figure 8. The distribution of microtine rodents vs. other prey on year (2018 and 2019). Whole model: N=406, $\chi^2 = 25.35$, df= 1, $p < 0.0001$.

Mountain hare was more common in the diet in 2018 than in 2019, accounting for 15.0% of the diet in 2018 and 4.3% of the diet in 2019 (Figure 9).

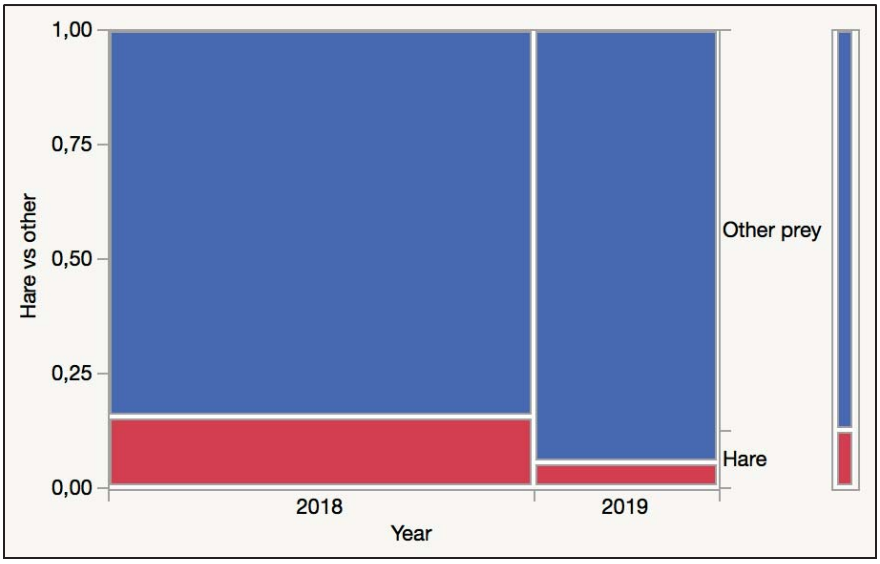

Figure 9. The distribution of mountain hare vs. other prey on year (2018 and 2019). Whole model: N=406, χ^2 = 7.58, df= 1, p= 0.0059.

The delivering sex

The sex of the delivering parent was determined for 444 of the 456 prey deliveries at the four nests. The male delivered a larger proportion (63%) of the prey items to the nests than the female (37%). The male delivered 77% of the total number of birds delivered at the nests (Figure 10). A total of 80% of the prey items delivered by the male were birds. The male delivered 86% of the total number of willow grouse and 68% of the thrushes delivered at the nests. The female delivered the major part (69%) of the mammals brought to the nests (Figure 10). The female delivered 90% of the microtine rodents brought to the nests (Figure 11), respectively 95% of the Norway lemmings and 79% of the *Microtus* sp. The parents brought equal numbers of both mountain hare and domestic sheep to the nests.

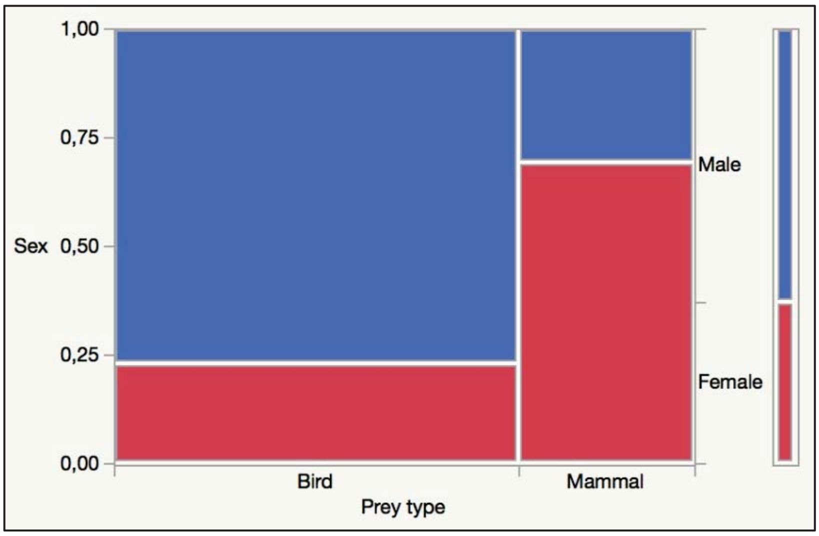

Figure 10. The distribution the delivering parent on main prey type (bird or mammal) delivered at four golden eagle nests. Whole model: N=419, $\chi^2 = 80.15$, df= 1, $p < 0.0001$.

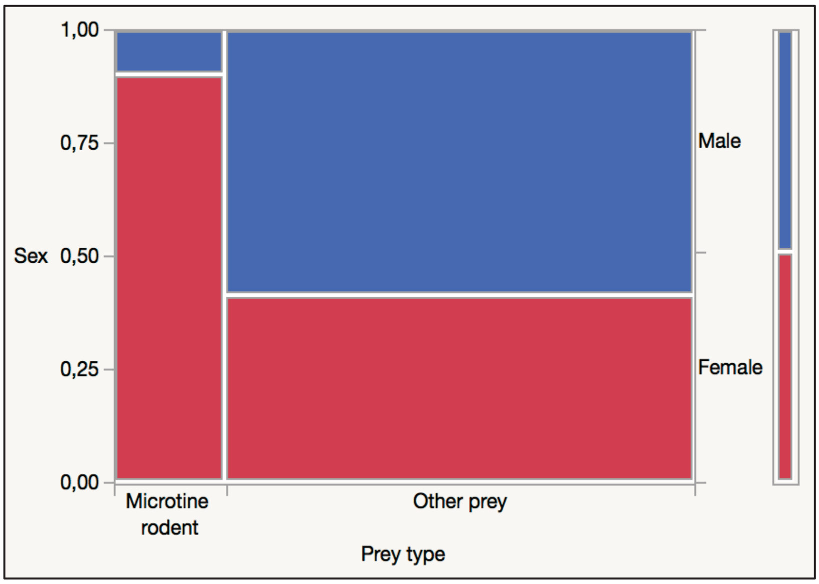

Figure 11. The distribution the delivering parent on prey type (microtine rodent or other prey) delivered at four golden eagle nests. Whole model: N=265, $\chi^2 = 38.94$, df= 1, $p < 0.0001$.

Factors potentially affecting the probability of the female being the delivering parent, were nestling age and gross prey body mass. Based on Akaike weights (Table 3), model 2 was likely to be the best fitted model and was selected to be tested further. Model 2 included the delivering parent, nestling age and nest ID.

In the beginning of the nestling period the females spent most of the time at the nest brooding and taking care of the nestlings, while the males was mostly out hunting and providing food for the female and nestlings. As the nestlings grew older the female spent more time away from the nest and contributed significantly more in the hunting in order to satisfy the dietary requirements of the nestlings (Figure 12, Table 4).

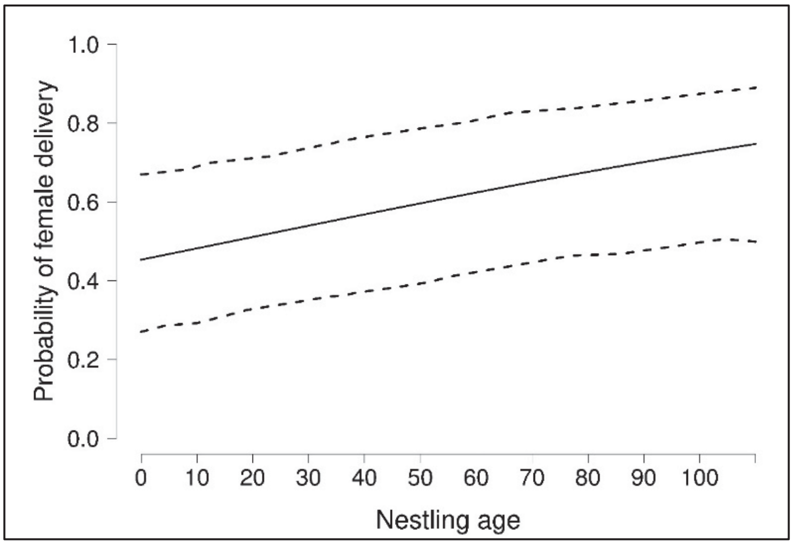

Figure 12. The probability of the golden eagle female delivering a prey item at the nest in relation to nestling age, represented by the black solid line. The upper and lower 95% confidence intervals are represented by the upper and lower dashed lines.

Table 3. Output of the model selection based on AIC analysis for models of factors affecting the probability of the golden eagle female delivering a prey item at the nest, with AIC values together with ΔAIC and AIC-weight.

Model	Variables	K	AIC	ΔAIC	AIC-weight
2	Delivering parent + Nestling age + ID	3	411.78	0.00	0.50
4	Delivering parent + Nestling age * Gross prey mass + ID	5	413.33	1.55	0.23
1	Delivering parent + Nestling age + Gross prey mass + ID	4	413.48	1.70	0.21
3	Delivering parent + Gross prey mass + ID	3	416.26	4.48	0.05

Table 4. Parameter estimates for the supported model (i.e., lowest AIC score in Table 3 – here model 2) fitted to predict the probability of female being the parent delivering a prey item at the nest.

	Estimate	Std. Error	z value	p
(Intercept)	-0.18795	0.60482	-0.311	0.7560
Nestling age	0.01154	0.00539	2.141	0.0322 *

Prey handling prior to delivery at the nests

After excluding the prey items for which it was impossible to determine the status of handling prior to delivery, 357 prey items remained. Out of these a total of 32.5% were decapitated and 18.8% were eaten at prior to delivery. For birds 32.5% were decapitated, 10.7% were eaten at and 32.9% were plucked prior to delivery. For mammals 33.6% were decapitated and 35.3% were eaten at prior to delivery.

Factors potentially affecting the probability of a prey item being decapitated prior to delivery at the nest were nestling age and gross prey body mass. Based on Akaike weights (Table 5), model 1 was likely to be the best fitted model. Model 1 was therefore selected to be tested further. Model 1 included the nestling age, gross prey body mass, whether the prey item was decapitated prior to delivery and nest ID.

Table 5. Output of the model selection based on AIC analysis for models of factors affecting the probability of a prey item being decapitated prior to delivery at the nest, with AIC values together with ΔAIC and AIC-weight.

Model	Variables	K	AIC	ΔAIC	AIC-weight
1	Decapitated + Nestling age + Gross prey mass + ID	4	377.39	0.00	0.51
4	Decapitated + Nestling age * Gross prey mass + ID	5	378.64	1.24	0.27
3	Decapitated + Gross body mass + ID	3	379.07	1.67	0.22
2	Decapitated + Nestling age + ID	3	453.38	75.98	0.00

The probability that a prey item was decapitated prior to delivery at the nest increased significantly with increased gross prey mass. In addition, there was a clear trend (almost significant) that the probability of decapitation decreased as the nestling became older (Table 6, Figure 13).

Table 6. Parameter estimates for the supported model (i.e., lowest AIC score in Table 5 – here model 1) fitted to predict the probability of a prey item being decapitated prior to delivery at the nest.

	Estimate	Std. Error	z value	p
(Intercept)	-1.162799	0.350062	-3.322	0.00090 ***
Nestling age	-0.010937	0.005742	-1.905	0.057
Gross body mass	1.178681	0.180107	6.544	< 0.001 ***

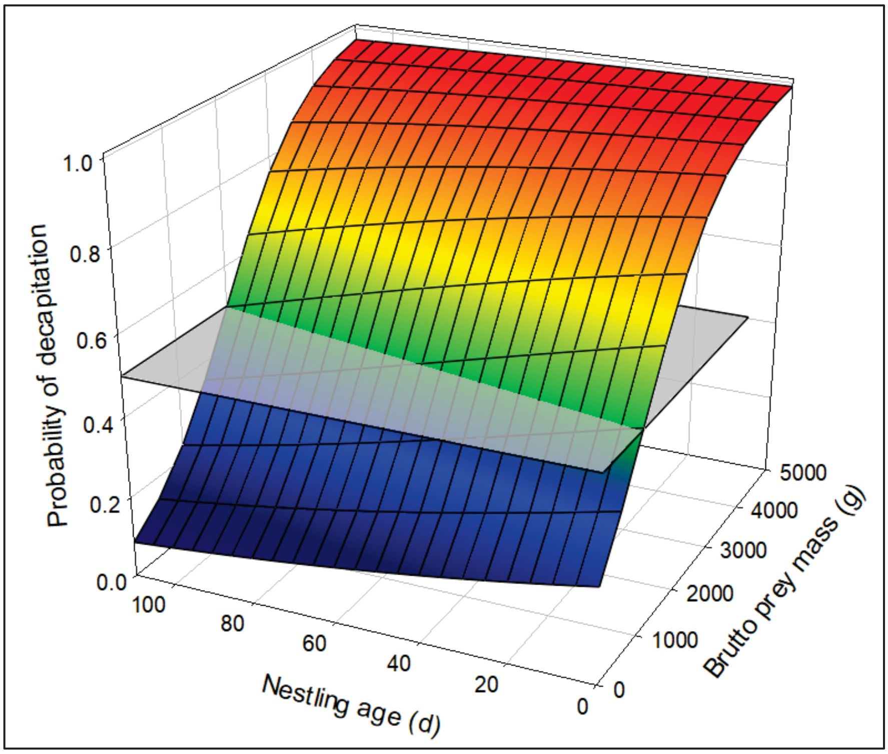

Figure 13. The probability that a prey item was decapitated prior to delivery at a golden eagle nest as a function of the age of the nestling (days) and brutto (gross) prey body mass (g). Note the reverse orientation of the scale along the axes.

Prey handling at the nests

Factors potentially affecting the probability of the nestling feeding unassisted, rather than being fed by the female, were nestling age and net prey body mass. Based on Akaike weights (Table 7), model 1 and model 4 were likely to be the best fitted models. I chose model 1 to be tested further because it had the lowest number of parameters. Model 1 included the nestling age, net prey mass, feeder and nest ID.

Table 7. Output of the model selection based on AIC analysis for models of factors affecting the probability of a prey item being eaten by the nestlings unassisted rather than being fed assisted by the female, with AIC values together with ΔAIC and AIC-weight.

Model	Variables	K	AIC	ΔAIC	AIC-weight
1	Nestling age + Net prey mass + Feeder + ID	4	162.97	0.00	0.56
4	Nestling age * Net prey mass + Feeder + ID	5	163.47	0.50	0.44
2	Nestling age + Feeder + ID	3	183.35	20.38	0.00
3	Net prey mass + Feeder + ID	3	450.18	287.21	0.00

The female was the only parent participating in the feeding and was recorded feeding for the majority of the prey items (57%). During the beginning of the nestling period the nestlings were always fed by the female. The probability that the nestlings fed unassisted increased significantly with increased nestling age (Table 8). The nestlings started feeding unassisted when they were on average 44 days old (range 36-55). After about 50 days there was a shift and it became more likely that the nestling fed unassisted than being fed by the female. This shift came earlier for smaller prey items than for larger prey items were the shift was after around 65 days (Figure 14).

Table 8. Parameter estimates for the supported model (i.e., lowest AIC score in Table 7 – here model 1) fitted to predict the probability of a prey item being eaten by the nestling unassisted rather than being fed assisted by the female.

	Estimate	Std. Error	z value	p
(Intercept)	-8.4919843	1.1416154	-7.439	$1.02e^{-13}$ ***
Nestling age	0.1859260	0.0215434	8.630	< 0.001 ***
Net body mass	-0.0016077	0.0003939	-4.081	0.000045 ***

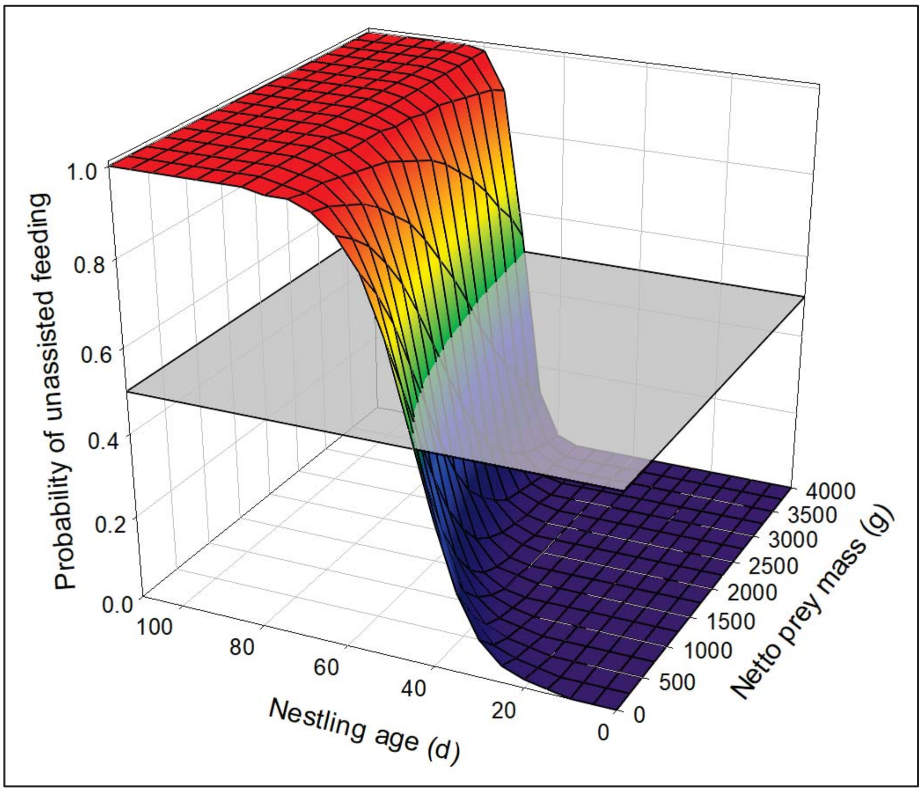

Figure 14. The probability that the golden eagle nestling fed unassisted as a function of age of the nestling (days) and net prey body mass (g). Note the reverse orientation of the scale along the axes.

Cleaning of the nest during the nestling period

On several occasions during the nestling period, the eagles were recorded removing leftover prey remains from the nests. Both smaller prey remains like feathers, skin and guts as well as larger prey remains like bones and legs from ungulates were observed picked up by the parent eagles and carried out and away from the nests.

In autumn 2019, I visited the nest where multiple parts from two domestic sheep were recorded delivered during the nestling period of 2018. Feathers from willow grouse and Northern hawk owl were found in the nest, but no remains from the domestic sheep. This was as expected since the eagles were recorded removing leftover prey remains multiple times during the video monitoring period. In contrast, the sheep leg delivered at the nest in 2019 was found at the nest when visiting in the autumn the same year.

Discussion

Prey delivered at the golden eagle nests

Out of a total of 456 prey items recorded delivered at the four golden eagle nests, the diet consisted of 64.8% birds, 29.5% mammals, 0.6% reptiles, 0.2% amphibians and 4.6% prey items could not be identified to a prey group. Birds being the most common prey type by numbers corresponds to other studies on the diet of golden eagles in Fennoscandia (Nyström et al. 2006; Skouen 2012; Nygård 2015). In terms of net biomass delivered at the nests, mammals were the most common prey group, accounting for 56.5% while birds accounted for 43.4%. The fact that birds comprised the most important prey group by numbers, but mammals still comprised the most important prey group by net biomass, corresponds with the results from two out of the three other studies using video monitoring as method in Norway, and these two were done in the same area as my study (Dihle 2015; Nygård 2015).

I estimated the average gross body mass of the prey at the time of capture to be 737 g. This is a bit lower than what Nygård (2015) found, namely 912 g. The average net body mass of all the prey items delivered was estimated to be 532 g. This was a bit higher than found in the three other studies done in Norway using video monitoring; Skouen (2012), Dihle (2015) and Nygård (2015) calculated the average net prey mass to be 493 g, 422 g and 448 g, respectively. In terms of biomass, mountain hare was the most common prey species accounting for 41.8% of the total estimated net body mass delivered at the nests, followed by willow grouse with 27.6%.

Watson (2010) stated that the typical range in size of prey items in the diet of golden eagles was 0.5-4 kg. I found a size range from a viviparous lizard estimated to weigh about 10 g up to a badger that was estimated to weigh about 4 kg. I recorded a larger proportion of smaller prey items than what has been found studies using traditional methods (Tjernberg 1981; Hagen 1952; Watson 2010). However, my results correspond well with those from the other three studies from Norway using video monitoring (Skouen 2012; Dihle 2015; Nygård 2015).

The main prey species by numbers were willow grouse accounting for 25.0% of the total numbers of prey items followed by thrushes (16.7%) and mountain hare (11.2%). The fact that willow grouse was the most common prey species was as expected because willow grouse is well known from previous studies to be an important prey species in the diet of golden eagles in Fennoscandia (Hagen 1989; Nyström et al. 2006; Johnsen et al. 2007). Results from line transect counts done by the local property management indicated an increasing population of willow grouse in my study area during my study (2018-2019) compared to the previous couple of years. The counts estimated a population density of approximately 12 willow grouse per km^2 in both 2018 and 2019 (Hønsefuglportalen 2020). This supports the high number of willow grouse I found in the diet. Watson (2010) found that the result from grouse transect count one year is a relatively good estimate on the number of grouse in the diet of the golden eagles the same year. This corresponds with my results but differs from the other studies from Norway using video monitoring, which did not find a relationship between the assessed willow grouse population in the area and the number of grouse recorded delivered at the golden eagle nests (Skouen 2012; Dihle 2015; Nygård 2015). Anyway, more data is necessary to conclude how correlated the assessed willow grouse population is with the proportion of willow grouse found in the diet of the golden eagles the same year in the same area.

Thrushes were the second most numerous prey species group in the diet. The high amount of thrushes in the diet corresponds well with data from the other studies in Norway using video monitoring (Skouen 2012; Dihle 2015; Nygård 2015). However, in previous studies using the more traditional methods, thrushes were almost absent (Hagen 1952; Sulkava et al. 1999; Nyström et al. 2006; Johnsen et al. 2007).

Microtine rodents, including Norway lemming and *Microtus* sp., accounted for 11.2% of the diet by numbers in my study. All were recorded delivered at the nests during the nestling period in 2018, when the population of microtine rodents was very high in the study area. In contrast, 2019 was a year with very low population of microtine rodents in the study area (Geir A. Sonerud, pers. comm.). This was well reflected as no microtine rodents were recorded delivered at the nest in 2019. The large difference between the number of microtine rodents delivered in 2018 and 2019 may indicate a functional response to the large populations of microtine rodents available in 2018. Dihle (2015) found the same response where microtine rodents accounted for 29.2% of the diet in the peak year for microtine rodents in 2014. Microtine rodents may be a more important source of food for the golden eagles than earlier assumed, at least in peak years where microtine rodents are abundant.

Traditional methods used to study the diet of raptors are often based on prey remains found in the nest. Studies comparing the traditional methods and video monitoring have found a potential bias with the former; large prey items seem to be overrepresented while small prey items are underestimated when using the traditional methods (Lewis et al. 2004; Tornberg & Reif 2007). One reason why this can be a problem is that smaller prey items can be swallowed whole and do not leave any remains in the nest. Another reason can be that prey items may be prepared prior to delivery at the nests or the eagles may clean the nest for prey remains during the nestling period (pers. obs). Therefore, the importance of some types of prey, particularly smaller prey items, in the diet of golden eagles is poorly understood from previous studies using the traditional methods. Video monitoring therefore seems to be a more reliable method to study the diet of raptors during the nestling period than the traditional methods (Lewis et al. 2004; Tornberg & Reif 2007).

Domestic sheep as prey

I recorded parts from a total of four domestic sheep delivered at three of the four nests studied. Each time a part of sheep was delivered it was one leg, sometimes with some extra meat attached to it, that was brought to the nest. Based on the size of the legs it is likely that the parts were from lambs and not adult sheep. To the best of my knowledge, I am the first in Norway using video monitoring to record parts of domestic sheep in the diet of golden eagles during the nestling period. However, other studies from Fennoscandia have found remains from both domestic sheep and domestic reindeer when examining prey remains and food pellets collected from golden eagle nests (Hagen 1952; Sulkava et al. 1999; Johnsen et al. 2007; Nyström 2006; Watson 2010).

In Norway there is a long tradition for summer pasture farming, where domestic livestock are released to outlaying grazing areas in the mountains and in forests, often quite far away from humans. This tradition comes with the potential cost that domestic livestock can be taken by predators. This has been a challenge in some areas where domestic livestock and predators coexist.

Each year the Norwegian government pays compensation to livestock farmers for lost income due to predation from predators, including the golden eagle (Rovbase 2020). During the grazing season for sheep in 2018 and 2019, a total of 51 lambs were compensated for in my study area in Gausdal and Sør-Fron municipalities due to assumed predation from golden eagles (Rovbase 2020). The numbers were distributed like this; 21 lambs in Gausdal municipality in 2018 and 11 lambs in 2019, while there was no lamb compensated for in Sør-Fron municipality in 2018, but 19 lambs in 2019 (Rovbase 2020). The golden eagle was held responsible for 30% (N=106) of the total cases of domestic sheep lost to predators in Gausdal and Sør-Fron municipalities during 2018 and 2019. Although rare and in low numbers, other big carnivores in addition to the golden eagle may be present in the study area. Both wolverine (*Gulo gulo*), wolf (*Canis lupus*), lynx (*Lynx lynx*) and brown bear (*Ursus arctos*) can be responsible for loss of livestock in the area. The lynx was responsible for the highest number of lost domestic sheep (41%) that were compensated for in the study area during the study period (Rovbase 2020).

Even though remains from domestic sheep were recorded delivered at the nests one cannot conclude that these sheep were killed by the eagles, because the sheep may have died of other causes and then been found by the eagles as carrion. Golden eagles are capable of catching prey the size of a lamb, but they are also known to eat a lot of carrion, especially during winter (Sánchez-Zapata 2010; Watson 2010). More research is needed to confirm whether the eagles are responsible for the death of the lambs. Still, most of the sheep lost during the period of summer pasture in Norway dies from other reasons than predation from predators, for example accidents or disease (Mattilsynet 2019).

The golden eagle's impact on domestic livestock has been a source of conflict and heated debate in some areas. One problem has been the lack of documentation in cases where the golden eagle has been accused for predation on livestock. Heggøy & Øien (2014) pointed out that in many cases compensation for lost livestock, mostly sheep and reindeer, were granted despite lack of documentation. This could contribute to give the golden eagle an undeserved bad reputation which can influence negatively on the conservation work for the species.

Most cases of lost livestock due to predation from golden eagles are reported early in the grazing season (June) when the lambs are small and have just recently been released to the summer pastureland. Gjershaug & Nygård (2003) also found a trend that golden eagle attacks often involved populations of sheep in poor condition which makes the lambs an easier prey. In my study the sheep delivered at the nests were delivered on the 6th, 17th and 28th of June in 2018 and on the 20th of July in 2019. Domestic sheep in the study area are released at the summer pasture sometime in early June.

Innlandet county (Hedmark and Oppland counties merged from 2020) makes up the largest summer pasture region in Norway. About 350,000 domestic sheep spent 12-16 weeks on summer pasture here during the summer of 2018. About two thirds of these was in former

Oppland county, where the numbers of sheep have increased during the last decade (Landbruksdirektoratet 2020). The total number of sheep compensated for due to predation from predators in Innlandet county during 2018 and 2019 were 9366 (Rovbase 2020). Out of these, golden eagles were held responsible for 427 cases (4.6%), and all of these were lambs. The predator in Innlandet responsible for most sheep lost to predators in 2018 and 2019 was wolverine, responsible for 48.6% of all cases, followed by the wolf (21.4%), the lynx (12.6%) and the brown bear (9.5%) whereas 3.4% remained unspecified (Rovbase 2020).

Delivery patterns for the main prey types

I found that the eagles were active all day long and that prey deliveries were recorded in 22 out of the 24 hours of the day. Summer nights in Norway are short and there are only a few hours when there is too dark for the eagles to be active. However, prey deliveries were most likely between 08 hours in the morning and 19 hours in the evening. The earliest prey delivery was recorded at 03:48 and the latest was recorded at 00:19. Golden eagles are known to be diurnal birds (Watson 2010), so my results were as expected.

I found that birds were delivered with equal probability throughout the day from about 09 hours until about 18 hours, while mammals tended to have a peak in probability of delivery in the morning and again a peak in the evening. This pattern was repeated when examining two of the main prey species, namely willow grouse and mountain hare. Willow grouse were delivered throughout the whole day while mountain hare had a peak in deliveries in the morning and again a smaller peak in the evening. This corresponds with the activity pattern of the prey species; willow grouse are diurnal while mountain hares are nocturnal and mostly active from the evening and throughout the night until next morning.

Differences in the diet between the nestling periods of 2018 and 2019

I found that the proportions of the different prey groups in the diet differed between the two study years. Notice that I only studied three nests in 2018 and one nest in 2019 so one should be careful concluding too firmly from these results. Ideally, one should have more data from multiple nests to fully compare two years. Anyway, it is still interesting to see the differences in the diet between the two years. Especially in this case, where 2018 was a peak year for microtine rodents in the study area while 2019 was the complete opposite with low populations of microtine rodents. Peak years for microtine rodents are known to have a great impact on the breeding success of many predators like hawks, falcons and owls, and also mammalian predators like foxes (*Canidae* sp.), stoat (*Mustela erminea*) and pine marten (*Martes martes*) (Selås 2020). Dense populations of microtine rodents can lead to decreased predation pressure on other species that are normally considered prey for many of the same predators mentioned above. In other words, a peak year of microtine rodents can result in a successful breeding season for many species, not only predators, but also species that are usually under a high predation pressure (Wegge & Storaas 1990). One example of a species that can benefit from this is the willow grouse, which is one of the most common prey species of the golden eagle in Fennoscandia (Watson 2010).

Golden eagles are known to be opportunistic hunters able to capture many different types of prey species (Watson 2010). How the diet of golden eagles across its range changes between habitats and seasons, according to what prey species that are available, shows how well adapted golden eagles are to different environments and proves its place on top of the food chain (Watson 2010). Nyström et al. (2006) found that the breeding success of golden eagles in northern Sweden showed a strong relationship to the yearly density index of willow grouse, which was the most important prey species. My results relate to this, as it seems that the eagles respond functionally to abundant population of prey species within their territories. I found a large proportion of willow grouse in the diet when the population of willow grouse in the area was estimated to be higher than in the last couple of years. Also, I found a relatively large proportion of microtine rodents (Norway lemming and *Microtus* sp.) in the diet during the nestling period of 2018, which was a peak year for microtine rodents in the study area. In contrast, no microtine rodents were recorded delivered at the nest in 2019 when the population of microtine rodents was estimated to be very low after a population crash between the two seasons (Geir A. Sonerud, pers.comm.).

The delivering sex

The distinctive parental roles were also present in the delivery rates of prey items at the nests. The male delivered 63% of all the prey items at the four golden eagle nests. The male is spending most of its time hunting and providing food for the female and nestlings, while the female spends much more time at the nest (Watson 2010; Sonerud et al. 2014). As the nestlings grow older, they need more food, and the female starts spending more time away from the nest and contributes in hunting and providing food for the nestlings (Sonerud et al. 2014). This is supported by my results. As the nestlings grow older, the probability that the female delivered prey at the nest increased.

However, one would might expect this pattern to be even clearer because the female spends so much time at the nest when the nestlings are small and still need a lot of care and brooding.

Sometimes when the male approached the nest with a prey item, the female left the nest, met the male and received the prey out of view from the camera. This phenomenon was observed live with binoculars at a distance from the nest in 2019 early in the nestling period. The male eagle approached the nest with the back part of a mountain hare, but before it had time to land, the female left the nest and they exchanged the prey outside the nest before the female eventually brought it to the nest and fed the nestling.

This behavior may be one of the reasons why it seems like the female hunted more prey than she actually did. To check how common this behavior is one need to register how much time the female spends away from the nests before it returns with a prey item. In this way one can see if it is likely that the female has caught the prey item itself, or if it is more likely that it was caught by the male. Another way to study this behavior is to observe from a distance with binoculars as Sonerud et al. (2013) did when studying this behavior in Eurasian kestrels (*Falco tinnunculus*). They found that the male selectively allocated larger prey items to the female for further prey handling and feeding of the nestlings, while smaller prey items were delivered directly to the nestlings (Sonerud et al 2013).

In my study the males delivered a total of 77% of the birds delivered at the nests, while the female delivered 69% of the mammals. This may be explained by the fact that males are smaller than females in order to be more effective when hunting for smaller, more agile prey items (e.g. birds). This hypothesis was presented by Slagsvold and Sonerud (2007). In fact, the female golden eagle can weigh as much as 50% more than the male and has a 10% longer wingspan (Watson 2010). This is called reversed size dimorphism (RSD) and is common among raptors, but in contrast to almost all other birds (Newton 1979). The size difference between the sexes make them adapted to hunt different types of prey and this may explain the differences in the proportion of different prey species delivered from each sex in my study.

Prey handling prior to delivery at the nests

A total of 32.5% of the prey items were decapitated and 18.8% were eaten at prior to delivery at the nests. The probability of a prey item being decapitated was the same for birds and mammals, but mammals had a greater probability of being eaten at than birds, 35.3% versus 10.7% respectively. The fact that the probability of decapitation was the same for birds and mammals contrasts with what Skouen (2012) found in golden eagles and what Steen et al. (2010) found when studying the Eurasian kestrel, namely that the probability of a prey item being decapitated was greater for birds than for mammals. My results showed that the probability of prey handling prior to delivery increased with the gross prey body mass. This is consistent with the feeding constraint hypothesis that states that small gape size limit young nestling from swallowing skulls (Slagsvold & Wiebe 2007; Steen 2010). Gape size is age dependent, therefore it was expected that the probability of decapitation decreased with nestling age and increased with gross prey body mass.

Golden eagles are constrained to their nest location throughout the breeding season and need to travel the distance between the nest and where they catch the prey many times in order to satisfy the hungry nestlings (Sonerud 1992). The eagles would need several small prey items to obtain the same amount of energy as one larger prey item. At the same time larger prey items require more handling time and more energy is used in order to bring it back to the nest (Slagsvold & Sonerud 2007; Slagsvold et al. 2010).

Prey handling at the nests

The female was the only parent feeding the nestlings at the nests. This was expected because raptors, including the golden eagle, are known to have quite distinct parental roles at the nest where the female is usually the only parent brooding and feeding the nestlings while the male is providing most of the food (Sonerud et al. 2014).

In the beginning of the nestling period the nestlings are dependent on the female to ingest food (Watson 2010). In my study the female assisted feeding the nestlings with the majority of the prey items (57%). Preparation of the prey before feeding it to the nestling includes using its sharp beak to remove inedible parts like for example the head or feathers on birds. Then the prey item is teared up in smaller parts which is then served to the nestling piece by piece and then swallowed whole (Slagsvold & Sonerud 2007).

The earliest case of unassisted feeding was when a viviparous lizard was delivered at one of the nests and the nestling swallowed it whole. At this time the nestling was estimated to be 22 days old. However, this case is not representative, because the prey item was very small, and the nestling was able to swallow it in one piece. The next time the same nestling fed unassisted it was 55 days old. From then on it regularly fed unassisted. In another nest, a nestling estimated to be 36 days old fed unassisted on an unidentified bird delivered by the male. The prey was decapitated and plucked prior to delivery. This was the earliest recorded case where a nestling fed unassisted and had to tear the prey item apart into pieces of a size it was able to swallow. On average, in the four nests studied the nestlings started feeding unassisted when they were estimated to be 44 days old. After about 50 days, it became more likely that the nestling fed unassisted than being fed by the female. This shift occurred earlier for smaller prey items than for larger prey items. This is very similar to what Dihle (2015) and Nygård (2015) reported, where the corresponding shift was after 49 and 47 days respectively.

Cleaning of the nest during the nestling period

Multiple times during the nestling period, I observed that the eagles removed prey remains from the nests. This could result in a bias in previous studies examining the diet of golden eagles, and other raptors, by traditional methods. Scientists often visited the nests after or during the breeding season to collect and analyze prey remains and pellets from the nest. Both small and large prey items can be underestimated, or not recorded at all, because there are no remains left in the nest. For example, I recorded that remains from large prey items (e.g. sheep legs) were removed from the nest by one of the adult eagles. On the other hand, small prey items (e.g. lizards) may leave no remains at all.

It is not known why the eagles remove prey remains from the nest. However, one possible reason may be to prevent unwanted attention from scavengers that can be a threat for the nestlings when they are still young. Also, some cleaning of the nest may reduce the number of insects at the nest which can be annoying for the eagles if they are abundant inside the nest. I was unable to find any other studies describing similar behavior where golden eagles clean the nest during and after the nestling period.

Biases and implications

I video monitored four golden eagle nests throughout the nestling period in the same general area in Norway, so my results may only reflect the diet during the nestling period and in this particular area. The golden eagle is a widespread generalist raptor known to have taken about 400 different vertebrate species (Watson 2010). Therefore, the golden eagle's diet can vary widely across its distribution range with local adaptations and specialization on different types of prey species as a response to variation in prey availability within their territories. Anyway, the results from my study should be representative for the diet of golden eagles living in mountainous areas of Norway and the rest of Fennoscandia and northern Europe but should be used with care outside this area due to variation in the availability of prey species.

Golden eagles typical nest far away from humans and can be sensitive to human disturbance during the breeding period. To minimize disturbance, we therefore installed the cameras at the nests prior to the breeding season (during autumn) when the eagles do not use the nests. One limitation with this method is that you are not sure whether there will be breeding at the nests where you have installed cameras at before you check status again in mid-May. Where and when a pair will breed can be challenging, especially since pairs of golden eagles are known to not breed every year and the fact that they can use different nests within their territories between years. If there is no activity when you check status in spring, you won't get any data from that season when using this method. Still, the wellbeing of the eagles should be your number one priority. Therefore, to increase the probability of breeding at a nest with camera installed, one should rather increase the number of nests with camera than to disturb the eagles during the breeding season. Installing a new camera at a nest in the middle of the breeding season can risk ruining the whole breeding season for the eagles by climbing the nest when the nestlings are young and vulnerable. Note that you also need a permission to study golden eagles with cameras at the nest, at least in Norway, because it is a protected species vulnerable to human disturbance and that wildlife in general are protected by law during the breeding season.

The cameras and video cable to the base station are standing outside through the whole winter and there is a risk that unwanted things can happen to the equipment. At the nest with breeding in 2019, we experienced bad video signal due to rodents that had chewed on the video cable during the winter. We found out that the damage on the cable was too close to the nest in order to fix it without disturbing the eagles, so we just had to deal with a bit worse video signal than optimal. One possible way to minimize the risk of rodents chewing on the cable is to attach the cable up in trees between the nest and the base station in order to lift the cable off the ground so it is not that easily available for rodents.

If you first succeed installing a camera at a nest and breeding is confirmed, video monitoring is a great way of studying nesting golden eagles and other raptors for that matter. Video monitoring is a cost-saving and time-efficient method (Steen 2009) and you can collect a lot of data from the life of the breeding eagles that are not possible to get in any other way. Not only data regarding their diet but for all kinds of other aspects regarding the breeding period of golden eagles. However, identifications of prey items can be difficult even with video monitoring and sometimes completely impossible and some prey items remain unidentified for various reasons or may be incorrect identified due to human error. Also, video monitoring of nests might not be the best method studying golden eagles and their potential predation on domestic livestock. Even though I recorded parts of domestic sheep delivered at the nest, it is impossible to conclude whether the eagles killed these or if they found them already dead. Also, immature eagles are more likely to predate on livestock (Watson 2010).

Conclusion

I found that birds were the most numerous prey group at the four golden eagle nests studied using video monitoring in Oppland County, Norway during the nestling period of 2018 and 2019. The most common prey species by numbers was willow grouse. This was expected because willow grouse is known as an important prey species from previous studies in Fennoscandia, and because local censuses in the study area estimated a relatively dense population of willow grouse during the study period. Thrushes comprised the second most numerous prey group, while mountain hare was the third most numerous. By biomass, mammals were more important than birds, and mountain hare was the most important prey species followed by willow grouse. The results from my study are largely in accordance with earlier studies done on the diet of golden eagles in Norway using video monitoring. However, my study was the first in Norway using video monitoring to record domestic sheep delivered as prey at the nests. Parts from a total of four sheep were registered brought to three out of the four nests during this study. However, it is uncertain whether the eagles had killed the sheep themselves or simply found them as carrion and then brought parts back to the nest.

There were differences in the proportion of the different main prey species in the diet between the two study years. The first, 2018, was a peak year for microtine rodents in the study area, which was well reflected in the diet with microtine rodents accounting for 17.3% of the prey items by numbers. In contrast, no microtine rodents were recorded delivered at the nest studied in 2019. This suggests that the golden eagles respond functionally to the availability of microtine rodents in a peak year and that this prey group is more important than earlier assumed.

About a third of the prey items were handled prior to delivery at the nest. The male delivered most of the prey items to the nest while the female was the only parent assisting the nestling with feeding and brooding. When the nestlings were about 50 days old the probability that they fed themselves unassisted was greater than being fed by the female.

More studies using video monitoring as method are still needed to fully understand the diet of the golden eagle across its range and to understand the importance of different prey types in their diet, including domestic livestock. In addition, more studies using video monitoring should be conducted to study the differences found in the diet using video monitoring versus the traditionally methods that obviously have some limitations.

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