Norwegian University
of Life Sciences

Master's Thesis 2023 60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Prey selection and prey handling of the golden eagle (*Aquila chrysaetos)* investigated by video monitoring at the nest

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Ecology

Acknowledgments

This thesis concludes the work of my master's degree in Ecology at the Norwegian University of Life Sciences.

I want to extend my deepest gratitude to my supervisors, Ronny Steen and professor Geir A. Sonerud who have helped me throughout the entire process from technical help with the camera, support in the field, identifying prey items, statistical analyses, and feedback on my drafts. Also, I would like to thank Helge Grønlien for supplying local knowledge and assistance in the field, and Vidar Selås for help with identifying the more challenging prey items. I am especially grateful to my sister and my grandparents for providing me with a place to stay during my field work, and for their continued interest and support of my project. My friends and classmates at the study hall have been incredibly important to me, and their friendship and support have made my time here at NMBU both a fun and memorable experience.

This project received funding from the county governor of Innlandet and from Viltfondet under the Norwegian Environment Agency. Without financial support for equipment and travel I would not have been able to complete my field work.

Ås, May 2023

Runa Odden

Abstract

Using video monitoring at the nest, I investigated the prey choice and breeding behavior of a pair of golden eagles (Aquila chrysaetos). The nest was video monitored throughout the breeding season, starting on the 9th of May, and ending on the 29th of August 2022. During the study 283 prey items were recorded delivered at the nest and included 199 birds (70.3%), 74 mammals (26.1%), and 10 (3.5%) prey items that could not be identified to a taxonomic group. The most numerous prey types were thrushes (*Turdus spp*.), ptarmigans (*Lagopus spp.*), and mountain hares (*Lepus timidus*). The mountain hare was the most important species in terms of gross prey mass, followed by ptarmigans and western capercaillie *(Tetrao urogallus).* The probability of a prey being a thrush increased with nestling age, the probability of a prey being a ptarmigan decreased with nestling age, while the probability of a prey being a hare did not have a relationship with nestling age. Throughout the study the remains of five sheep (*Ovis aries*) were recorded being delivered at the nest. From the recordings it was not possible to determine if the sheep were killed by the eagles, or if they were found as carrion. The diel delivery pattern had two separate peaks, one in the morning and one in the evening, and a probability of delivery higher than randomly expected from 07 hours until 18 hours. The number of prey deliveries per day increased with nestling age, while the net prey mass delivered per day did not have a significant relationship with nestling age. The increase in prey deliveries was likely mitigated by a smaller mean mass per prey delivered as the nestlings aged and the female resumed hunting, resulting in the absence of a significant increase in delivered net mass per day. Additionally, the male delivered smaller prey than the female, delivering prey with a smaller gross mass as the nestlings aged. The female showed a tendency to deliver prey with a higher gross mass as nestlings aged. The probability of a prey being decapitated prior to delivery decreased with nestling age and increased with the gross mass of the prey item. Whether an avian prey was plucked prior to delivery was not related to gross prey mass. The probability of the nestlings handling a prey item unassisted increased with nestling age and decreased with the net mass of the prey item. Only the female assisted the nestlings with feeding and partitioning prey items. The female fed the nestlings or helped to partition prey for 60.4% of the delivered prey items. The first instance of a nestling feeding unassisted occurred when it was 36 days old, however, the nestlings did not feed unassisted consistently until much later. The nestlings handled the smallest prey (20g) unassisted more likely than not at an age of approximately 58 days. For average sized prey (487 g) they were more likely than not to handle unassisted at 78 days. The male was the primary provider of prey, as he delivered 87% of the prey items at the nest. The findings of my study support that the golden eagle is a generalist predator, capable of utilizing a wide variety of prey species and adapting to spatial and temporal variations in prey availability. The diet of the golden eagle also changed throughout the breeding season to allow nestlings to handle prey without assistance earlier, allowing the female to join the hunting effort. My study highlights the flexibility of the golden eagle as a predator and its main breeding behaviors at the nest.

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Introduction

Predators play an important role in the world's ecosystems. They occupy a high trophic level where they affect the distribution and abundance of individuals at lower trophic levels, either directly or indirectly (Barbosa & Castellanos, 2005) (Davies et al., 2012). As a top predator the golden eagle's abundance, distribution, and reproductive success is affected by the abundance of their prey species (Newton, 1979). However, generalist predators can switch between prey species as their abundance varies, to maximize net energy intake per time unit (Hanski et al., 1991). The foraging strategies and diet of raptors are altered during the breeding season to fulfill the needs of the nestlings and brooding female. Both parents are limited to areas closer to the nest to reduce travel time and selective provisioning is an important element for the reproductive success of a breeding pair (Stephens et al., 2007; Moss et al., 2012). When prey is detected, the parent must consider the energy content of the prey and the handling time to determine the most profitable option (Kaspari, 1990).

Raptors hunt large prey for their size, compared to other birds, which makes their prey selection less constrained. Their method for prey handling makes this possible, raptors use their sharp beak not to peck, but to tear their prey into smaller pieces (Slagsvold et al., 2010). Although time-consuming, this behavior allows a much broader niche of prey species that is not limited by prey size or the birds' own gape size (Kaspari, 1990). Most raptor species have reversed sexual size dimorphism, with a larger female (Newton, 1979; Slagsvold & Sonerud, 2007; Sonerud et al., 2014b). During the breeding season, the male mainly hunts and provides prey, while the larger female incubates the eggs, broods the nestlings, and feeds nestlings (Newton, 1979; Collopy, 1986; Watson, 2010). Later in the breeding season the female may contribute more to hunting as the nestlings are less vulnerable and simultaneously need more prey (Newton, 1979; Sonerud et al., 2014b). Prey selection, prey handling, and parental care at the nest changes with nestling age, and the type of prey delivered (Steen et al., 2010; Sonerud et al., 2014a).

The golden eagle (*Aquila chrysaetos*) is one of the largest birds of prey in the world and Norway's second largest raptor, only slightly behind the white-tailed eagle (*Haliaeetus albicilla*) (Halley, 1998; Watson, 2010). The geographical distribution of the species includes most of the Palearctic and northern Africa (Newton, 1979; Katzner, 2020). The preferred habitat is open forests and mountainous areas, and breeding pairs are distributed over large parts of Norway (Halley & Gjershaug, 1998; Watson, 2010; Mattisson, 2020). Like other raptors, the golden eagle exhibits reversed sexual dimorphism, with the female being larger than the male (Watson, 2010), with the female typically weighing around 5 kg and the male around 3.5 kg, with a wingspan of 175-205 cm (Watson, 2010). The golden eagle is a generalist that has a broad specter of prey species ranging from small and medium-sized birds and mammals to larger mammals including reindeer and domestic sheep (Nybakk et al., 1999; Warren et al., 2001; Nystrom et al., 2006; Johnsen et al., 2007). The killing of domesticated animals is highly controversial and has management implications for the species (Gjershaug & Nygård, 2003). In Norway, there are compensation schemes for livestock lost to wildlife and in 2022 the Norwegian government economically compensated farmers for a total of 1925 domestic sheep, and reindeer herders for 8127 semi-domestic reindeer, killed or damaged by the golden eagle (Rovbase, 2022a; Rovbase, 2022b). Historically, the golden eagle was heavily hunted in Norway with bounties paid by the government implemented in 1846 (Heggøy, 2014). The population steadily declined until the total protection of the species in 1968, per 2019 there are estimated between 914 and 1145 breeding pairs of golden eagles in Norway (Mattisson, 2020). The golden eagle has few natural predators and occupies a high trophic level. The main threats are man-made, from hunting, habitat destruction, disturbance, lead poisoning from carrion shot with lead bullets, and toxic waste reducing the thickness of eggshells leading to lower breeding success (Newton, 1979; Marquiss et al., 1985; Heggøy, 2015; Heggøy, 2020).

Historically, the diet and behavior of raptors have been explored using observational fieldwork, examining pellets, or examining carcasses and feathers at the nest or plucking sites (Tjernberg, 1981; Lewis et al., 2004; Watson, 2010). These methods are time consuming and often invasive for the species being studied. Additionally, the examination of pellets and carcasses can lead to biased results because both biomass and the number of prey are often underestimated, uncommon species are poorly registered compared to common species, and smaller prey are often underrepresented (Lewis et al., 2004; Harrison & Hallingstad, 2018). Such methods often involve human physical presence at, or near the nest, which can be very disruptive for both nestlings and parents (Whitfield et al., 2006; Heggøy, 2015). Advancement in technology has led to a surge in video monitoring in wildlife research and management (Boitani, 2016). Video monitoring allows insight into both raptor behavior and diet, especially during the breeding season (Lewis et al., 2004; Steen, 2009). Potential biases are reduced using this method, and prey handling can be viewed repeatedly to decide prey species and further examine nest behavior and provisioning. Further, video monitoring allows other factors such as time of day and time intervals between feedings to be explored (Lewis et al., 2004; Reif & Tornberg, 2006). However, monitoring at the nest also presents certain biases. Not all captured prey is necessarily delivered at the nest, and certain species may be overrepresented among the delivered compared to the captured prey (Sonerud, 1989; Sonerud, 1992). Further, smaller prey items may be swallowed by the parents before delivery, meaning there is a potential for smaller prey also being underestimated in the diet when using video monitoring.

The use of video monitoring at the nest during the breeding season allows further knowledge of prey selection and prey handling, both prior to delivery and in the nest. Constant video surveillance by motion detection also gives the opportunity to investigate how the time of day affects prey selection and prey availability and the amount of prey being delivered each day (Steen, 2009). Video monitoring can help mitigate biases from more traditional methods, allowing uncommon prey and smaller prey to be represented more accurately in the diet (Gjershaug et al., 2018). Furthermore, data on predation on livestock such as domestic sheep or domestic reindeer could be supplemented by this method.

In this master thesis I aim to investigate the following research questions: 1) What is the golden eagle's diet and prey selection during the breeding season? Determining the most important prey species or groups as well as the prevalence of predation on domestic sheep. 2) What is the level of handling, if any, of delivered prey and the level of parental care at the nest? 3) How does time of day affect the quantity of prey and/or the type of prey delivered to the nest? 4) How does nestling age affect what prey is delivered, the amount of prey delivered, and the amount of handling performed prior to delivery?

Material and methods

Study area

The study was conducted in 2022 in Innlandet County in South-Eastern Norway. The exact location is confidential. The study area is described by Landskap NiN (Landskap-NiN, 2023) as an open valley landscape beneath the tree line. The area contained vegetation typical for a boreal forest, with the dominant tree species being Norway spruce (*Picea abies),* Birch *(Betula pubescens),* and Scots pine (*Pinus Sylvestris)*. The golden eagle nest was situated in a south-facing cliffside, right beneath the tree line but in proximity to more mountainous areas. There was a road close to the nest, but human settlements in the study area were scarce. However, there were farmsteads with outdoor grazing livestock within the eagles' territory. Monitoring started May 9th when the nestlings were approximately 5 days old. There were two nestlings who fledged on the 26th of July and the 3rd of August, respectively. The first nestling that fledged returned to the nest several times until the second nestling fledged. Neither nestling nor parents returned after the 3rd of August, but the recording was left on until the battery depleted to see if any of the nestlings would return to the nest.

Video monitoring

Video monitoring was implemented to investigate the prey choice and behavior of the golden eagle at the nest during the nestling period. The method used is similar to the method described in Steen (Steen, 2009). The equipment used in the project was a CCTV camera with a wide-angle lens, mounted on a birch close to the nest. Via a 100 m long cable the camera was connected to a mini digital video recorder (mini-DVR) on the ground. The mini-DVR had a video motion detector (VMD) with an adjustable detection zone, which was set around the edge of the nest. During movements 10 seconds before and after events were stored on a 32-gigabyte SD card. The whole surveillance system was powered by a 12V (80Ah) deep cycle lead battery and a 100W solar panel. To avoid disturbing the eagles during the nesting period, the camera had been installed and checked in the previous fall. Disturbing the eagles when they are incubating on eggs or brooding young chicks might lead to them abandoning the breeding season, thereby killing the nestlings (Watson & Whitfield, 2002; Whitfield et al., 2006; Heggøy, 2015). Experience from previous seasons led me to trim or remove some deciduous trees as they started to obstruct the sun from the solar panel. This increased the panel´s ability to charge the battery during the study period.

The study site was visited every four to five days depending on the level of activity on the nest. At each visit to the site, the SD card was exchanged with a new one, and its contents were transferred to an external hard drive. Two SD cards were used as a precaution so no data would be lost when transferring in the field. The rest of the equipment was checked, and the quality of the camera was ensured using a portable LCD screen. The sensitivity of the VMD was set to seven in the first week, which was reviewed to be too sensitive for the camera angle, and therefore changed to nine for the rest of the study period. This alteration allowed more time before the SD card was filled up, without missing any prey deliveries or important activity on the nest.

During the field work I was presented with some technical difficulties. The camera angle was more head-on and closer to the nest than in previous years. Therefore, the sensitivity of the VMD was set too high for the first week, leading to the SD card filling up. After a period of heavy rainfall and high humidity, the mini-DVR started failing, leading to sporadic recordings and longer stretches of time, especially at night, where no videos were recorded. The cause of the problem was discovered, and a backup mini-DVR was installed, which remained functional throughout the rest of the study period. An unexpected challenge occurred when one of the nestlings defecated on the camera lens. The new camera position turned out to be too close to the nest and too low, allowing this to happen. Due to the properties of bird excrement, the camera lens was obscured, especially as the excrement solidified over time. Luckily, this was discovered only two days later, and due to the quick response from Helge Grønlien and climber Emil Haug, the problem was resolved the following day. The lens was washed by the climber and the camera was moved to a different branch higher up and further from the nest to prevent a repeat of the situation. Additionally, the solar panel did not generate enough electricity to power the battery for the entire field period. The 12-volt battery was changed towards the end of June and some trees at the study site were removed or trimmed to allow more sunlight to reach the solar panel. Video monitoring lasted 87 days, and during the study period about six days in total were not recorded or only partially recorded. There was a total of 47 768 recorded videos throughout the study period, and the recorded clips varied in length from the shortest 16 seconds to the longest around 16 minutes. Most clips ranged from 30 seconds to 1 minute. The camera was active for around 2280 hours, and approximately 399 hours of video were recorded.

Data collection and data processing

Data was collected using video monitoring, and the breeding diet was determined by registering all prey delivered to the nest. BORIS (Behavioral Observation Research Interactive Software) was used to view and collect the recordings that contained prey deliveries (Friard & Gamba, 2016). Each prey delivery was viewed several times, also frame by frame to determine prey species or family when exact species could not be determined. The prey was first sorted by their lowest taxonomic group and divided into mammals and birds. The sex of the parent delivering the prey was also determined. Golden eagles have reversed sexual size dimorphism with a larger female, and for the pair the male was also ringed, allowing the sex of the delivering parent to be determined. Additionally, the time of delivery was registered for each prey delivery. The level of prey handling prior to delivery was registered for each prey, and classified into no handling, plucked, headless, and partially eaten when delivered at the nest. The sex of the handling parent was also determined. For prey only handled by one or both parents, the handler was scored as parent handler. When prey was partially handled by the parent before the nestling began handling the handler was scored as both parent and nestling. Only when the nestling handled the prey without any assistance from parents the nestling was registered as the handler. Out of the 283 prey items delivered at the nest in my study 273 were determined to at least class, with 10 prey items where the taxonomic class was not possible to determine. Further, there was 41 prey items that were determined only to class, but not order, family or species. The remaining 232 prey items were determined to class and either order, family, or species.

The delivered prey items were assigned a gross and net mass when this could be estimated. The gross mass of prey was taken as the mass of the prey when it was captured by the eagle, while net mass was taken as the mass of the prey when it was delivered at the nest. The gross mass was set as the average body mass of that species from previous video monitoring studies (Günther, 2020; Mjelde, 2021), from the literature (Cramp, 1980; Cramp, 1983; Cramp, 1988; Cramp, 1993; Cramp, 1994) and G. Sonerud (Personal comm.). When the prey species was determined but the mass was not, the mean mass of that species was registered. This was necessary when, for example, the prey delivery itself was not recorded. In cases where prey could only be determined to bird or mammal the gross mass was estimated by comparing the size of the prey to the size of the golden eagle. For birds not identified to species 6 of 39 were registered as the mean gross mass for avian prey delivered, as it was difficult to estimate the body mass based on size. Some nestlings of thrushes were delivered and visually estimated to weigh 20 g each. The gross mass of the sheep remains delivered to the nest was not included because it was too difficult to accurately estimate the gross mass when so little of the animal was delivered at the nest. Consequently, for a spine belonging to an unidentified ruminant, likely a roe deer or a sheep, the gross and net mass was not included. The gross and net mass of one unidentified mammal and all ten unidentified prey items were not included for the same reason. The net mass of a prey item was determined from the state of prey items state on delivery. As several of the delivered prey items were partially eaten, the net mass was determined visually. I was assisted by Geir Sonerud and Vidar Selås in making these estimations. If a bird was decapitated prior to delivery, 12.9% of the gross mass was subtracted to find the delivered net mass (Sonerud et al., 2014b).

Statistics

Statistical analysis was performed using R version 4.1.1 (R Core Team, 2021), and the significance level was set to alpha = 0.05. Plots and graphs were made in R using packages ggplot2 (Wickham, 2016), overlap (Ridout & Linkie, 2009), activity (Rowcliffe, 2022), plotly (Sievert, 2020), and the base R function plot. The package AICcmodavg (Mazerolle, 2020) and tidyverse (Wickham H et al., 2019) were used to process data and perform statistical analysis.

I used generalized linear models (glm) to model the relationship between a response variable and explanatory variable(s). Linear regression was used when the response variable was continuous and normally distributed (Gaussian), logistic regression was used when the response variable was binary (binomial), and Poisson regression was used when the response variable was a count variable (Poisson distribution). I tested several candidate models with different combinations of explanatory variables, including interaction terms. Not all possible combinations were tested, but I chose the ecologically reasonable ones.

Akaike's information (AIC) was used to decide the best fitting model, by selecting the model with the lowest AIC. In order to find the best model, I tested reasonable ecological variables against each other and reviewed their AIC values (Akaike, 1974). The model with the lowest AIC score was selected as the best model, however, when the difference in AIC score between two models was less than two, they were considered indistinguishable from one another. In these instances, the model with the lower AIC score was not considered significantly better, and the most parsimonious model with the lowest K value was chosen. The model with the lowest K value is the model with the smallest number of parameters.

When examining the diel delivery pattern, each day was divided into 24 hour-blocks, and the probability of a prey being delivered in each hour-block was calculated from the delivery times using logistic regression. The response variable was the probability of prey being delivered for each hour-block, while the explanatory variable was time of day. For each hour-block the response variable had two possible outcomes, either no prey delivered or at least one prey delivered. The models with the lowest AIC score were selected as best fitting. The cosine curve fitting method (cosinor) was used (Steen, 2020). The diel pattern from the best fitting model was compared to the MESOR, the midline estimating statistic of rhythm. When the lowest 95% confidence interval was higher than the MESOR line, the delivery rate was significantly higher than randomly expected, and when the highest 95% confidence interval was lower than the MESOR line, the delivery rate was significantly lower than randomly expected. Candidate models are presented in Appendix A.

The activity distribution was calculated from the number of prey deliveries recorded in each hour over the course of the day. The frequency was higher when more prey were recorded, and lower, when fewer prey were recorded. The area under the distribution line suggests the prey availability of a certain species or group (Rowcliffe, 2022). Unlike diel delivery pattern plots, activity measures the frequency of prey delivery per hour block, not the probability. The overlap of prey deliveries throughout the day was explored using the overlap package in R. The package fits kernel density to times of events and estimates the coefficient of overlap. The overlap coefficient ranges from 0, no overlap, to 1, complete overlap. A bootstrap was performed to determine the precision of the overlap coefficient between the delivery density of different species (Frey et al., 2017). The method can be used to estimate activity patterns from camera trap footage and identify potential interactions, such as competition and predation. (Ridout & Linkie, 2009). My data are camera footage from a nest, so rather than observations of animals passing a camera trap, my observations are prey deliveries by the golden eagles. However, these data can indicate the availability of prey throughout the day and the difference between prey species' diel activity patterns.

Further, I wanted to explore which variables affected the number of prey deliveries, the gross and net mass delivered, and what type of prey were delivered. First, I tested whether the number of prey deliveries per day was affected by nestling age. Secondly, I tested whether the net prey mass delivered per day was affected by nestling age. Thirdly, I tested whether the gross mass of prey was affected by nestling age, sex of delivering parent, and the interaction term. Thirdly, I tested whether the probability of prey being a thrush instead of any other prey was affected by nestling age, and whether the probability of a prey being a ptarmigan was affected by nestling age, and whether the probability of a prey being a hare was affected by nestling age. For models including more than one variable, I used AIC score to select the best fitting model. The models that were tested as generalized linear models were tested without using AIC as I only wanted to investigate the effect of nestling age as the explanatory variable. These models are presented in Appendix C.

Additionally, I wanted to explore which variables affected prey handling prior to delivery at the nest, and the probability of nestlings handling unassisted. First, I tested whether the probability of prey being decapitated was affected by nestling age, sex of the delivering parent, gross prey mass, and the interaction term. Secondly, I tested whether the probability of nestlings handling prey unassisted was affected by nestling age, sex of the delivering parent, net prey mass, and the interaction term. Finally, I tested whether the probability of an avian prey being plucked prior to delivery at the nest was affected by nestling age, gross prey mass, net prey mass, and the interaction term. The models with the lowest AIC score were selected as the best fitting model.

Results

Prey delivered at the nest

During the study period the golden eagles were recorded to deliver 283 prey items at the nest, spanning over at least 23 prey species. The most numerous prey type were birds with 70.3% of all prey deliveries, while mammals made up 26.1% of all prey, and 3.5% of delivered prey items were unidentified (Table 1). The most common species of were thrushes (*Turdus* spp.), together accounting for 33.2% of all prey. The second most numerous prey species were ptarmigan (*Lagopus* spp.) with 14.8%, and the third most numerous species were mountain hares (*Lepus timidus*) with 11.7% of all prey deliveries. These three most numerous species collectively accounted for 59.7% of all prey, and 68.59% of net prey mass delivered at the nest. Apart from the species mentioned above, most species only accounted for a small proportion of prey items, as well as prey mass.

In terms of gross mass, the most important species was the mountain hare, accounting for 47.4% of the total gross mass (Table 1). The second most important prey species was ptarmigans with a total gross mass of 14.04%. The western capercaillie (*Tetrao urogallus)* only accounted for 1.77% of prey deliveries but was the third most important species in terms of gross mass with 9.98% of the total gross mass. Thrushes were the most numerous prey species but only accounted for 3.6% of the gross mass. For delivered net prey mass hares were still the most important prey type, accounting for 46.8% of all delivered prey mass. Ptarmigans were the second most important group with 14.63% of delivered net prey mass. The western capercaillie was the third most important with 7.3% of delivered net mass, followed by thrushes with 7.13% of delivered net mass.

Domestic sheep as prey

Domestic sheep (*Ovis aries*) parts were delivered at the nest on five separate occasions during the study period and accounted for 1.7% of all prey items. Only one leg or two legs connected at the hip were delivered. The parts were delivered on the 19th, 27th, 30th of June, and the 11th and 30th of July. Additionally, a spine was delivered, but it could not be determined if it was the spine of a roe deer or a sheep, and therefore this item was not included with the domestic sheep prey.

Table 1. Prey delivered to a golden eagle nest in the nestling period of 2022.

	Prey number		**Estimated gross body mass**			**Estimated net body mass**		
Prey species	**N**	**%**	**Per prey**	**All prey**	**%**	**Per prey**	**All prey**	**%**
Mallard (*Anas platyrhynchos*)	1	0.35	200	200	0.14	200	200	0.16
Ptarmigan (*Lagopus* spp.)	42	14.84	481[1]	19700	14.04	433[2]	17840	14.63
Western capercaillie (*Tetrao urogallus*)	5	1.77	2800[3]	14000	9.98	1780[4]	8900	7.30
Black grouse (*Tetrao tetrix*)	9	3.18	900[5]	8100	5.77	806[6]	6450	5.29
Grouse	1	0.35	200	200	0.14	200	200	0.16
Whimbrel (*Numenius* spp.)	2	0.71	325[7]	650	0.46	300	600	0.49
Eurasian woodcock (*Scolopax rusticola*)	2	0.71	300	600	0.43	280[8]	560	0.46
Common greenshank (*Tringa nebularia*)	1	0.35	170	170	0.12	170	170	0.14
Snipe (*Scolopacidae* spp.)	1	0.35	200	200	0.33	200	200	0.40
Sparrowhawk (*Accipiter nisus*)	1	0.35	250	250	0.18	200	200	0.16
Rough legged buzzard (*Buteo lagopus*)	1	0.35	980	980	0.70	500	500	0.41
Redwing (*Turdus iliacus*)/ Song thrush (*Turdus philomelos*)	2	0.71	70	140	0.10	70	140	0.11
Common blackbird (*Turdus merula*)	5	1.77	100	500	0.36	100	500	0.41
Common blackbird (*Turdus merula*)/ Ring ouzel (*Turdus torquatus*)	8	2.83	100	800	0.57	100	800	0.66
Thrush indet. (*Turdus* spp.)	79	27.92	93[9]	7388	5.27	91[10]	7242	5.94
Unidentified bird	39	19.60	213[11]	6515	10.79	117[12]	5135	10.35
Total bird	**199**	**70.32**	**7382**	**59545**	**43.05**	**5907**	**50305**	**40.71**
Mountain hare (L*epus timidus*)	33	11.66	2015[13]	66500	47.41	1730[14]	57100	46.84
Eurasian red squirrel (*Sciurus vulgaris*)	9	3.18	300	2700	1.92	277[15]	2200	2.05
Field vole/ tundra vole (*Microtus* spp.)	3	1.06	56[16]	170	0.12	56[17]	170	0.14
Vole (*Microtinae*)	16	5.65	50[18]	760	0.54	50[19]	760	0.62
Red fox (*Vulpes vulpes*)	1	0.35	2000	2000	1.43	2000	2000	1.64
Stoat (*Mustela erminea*)	3	1.06	250	750	0.53	250	750	0.62
Roe deer (*Capreolus capreolus*)	2	0.71	3500	7000	4.99	2000	4000	3.28
Sheep (*Ovis aries*)	5	1.77	-	-	-	1666	5000	4.10
Unidentified ruminant (*Ruminantia*)	1	0.35	-	-	-	-	-	-
Unidentified mammal	1	0.35	-	-	-	-	-	-
Total mammal	**74**	**26.15**	**8171**	**79880**	**56.94**	**8029**	**71980**	**59.29**
Unidentified prey	10	3.53	-	-	-	-	-	-
Total	**283**	**100.00**	**15553**	**140273**	**100.0**	**13636**	**121917**	**100.00**

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[1] Mean estimate, variation 100-500 g
[2] Mean estimate, variation 100-500 g
[3] Mean estimate, variation 2000-4000 g
[4] Mean estimate, variation 1000-2500 g
[5] Mean estimate, variation 750-1200 g
[6] Mean estimate, variation 500-1200 g
[7] Mean estimate, variation 300-350 g
[8] Mean estimate, variation 260-300 g
[9] Mean estimate, variation 70-100 g
[10] Mean estimate, variation 40-100 g
[11] Mean estimate, variation 25-500 g
[12] Mean estimate, variation 25-500 g
[13] Mean estimate, variation 1000-4000 g
[14] Mean estimate, variation 500-4000 g
[15] Mean estimate, variation 100-300 g
[16] Mean estimate, variation 50-70 g
[17] Mean estimate, variation 50-70 g
[18] Mean estimate, variation 30-70 g
[19] Mean estimate, variation 30-70 g

Proportion of prey

As the nestlings grew older the proportion of prey types in the diet changed. To explore this further, I divided the age of the nestlings into three equally sized groups. Throughout the study period birds were the most numerous prey type with 199 prey, representing 70.6% of all prey delivered to the nest and 72.6% of identified prey. However, their total net mass only represented 40.71% of the total net mass delivered. Mammals had a lower proportion of number of prey delivered at 26.15%, and 27.1% of identified prey, but represented the largest proportion of net mass delivered to the nest with 59.29% (Table 1). The nestling's age was divided into three age groups, 6-33 days old, 34-62 days old, and 63-91 days old (Figure 1). In the youngest age group ptarmigan was the most numerous prey type with 25.8% of prey representing 23.4% of the total mass delivered for this age (Figure 2). In the same age group thrushes were the second most numerous prey with 22.4% of prey, but their total net mass only represented 3.8%. Hares accounted for 15.5% of prey items in the same period but had the largest proportion of net prey mass with 45.4%.

In the middle age group when nestlings were 34-62 days old, ptarmigans were still the most important prey in terms of numbers with 25.0% of all prey (Figure 1), but accounting only for 19.7% of the prey mass (Figure 2). The second most numerous groups were thrushes with 20.0% of the numbers and 3.1% of the total prey mass. The third most numerous were hares with 12.5%, but still the largest proportion of mass delivered with 37.9%.

In the last age group when nestlings were 63-91 days old the proportion of prey changed compared to the first two periods. The most numerous prey group was thrushes with 45.1% of the delivered prey (Figure 1), accounting for 11.2% of the total mass delivered (Figure 2). The second most numerous prey type was hares with 9.7% of delivered prey, however, this prey type still contained the largest proportion of the delivered mass with 56.7%. The third most numerous prey type was voles with 6.2% of delivered prey, but only 0.81% of the delivered prey mass. Ptarmigans were the fourth most numerous prey in the oldest age group with 5.5% of delivered prey, and 6.4% of the delivered prey mass.

While birds had the largest proportion of prey deliveries for each age group, they did not represent the largest proportion of net prey mass delivered to the nest. Hares were the most important prey type in terms of net prey weight delivered, regardless of age group. The mean net mass of delivered hares was 1730.3 g with a minimum mass of 500 g and a maximum of 4000 g. (Table 1) For ptarmigans, the mean net mass delivered was 427.9 g with a minimum of 100 g and a maximum of 500 g (Table 1). The last major prey group is thrushes with a delivered mean net mass of 92.4 g with a minimum of 40 g and a maximum of 100 g (Table 1).

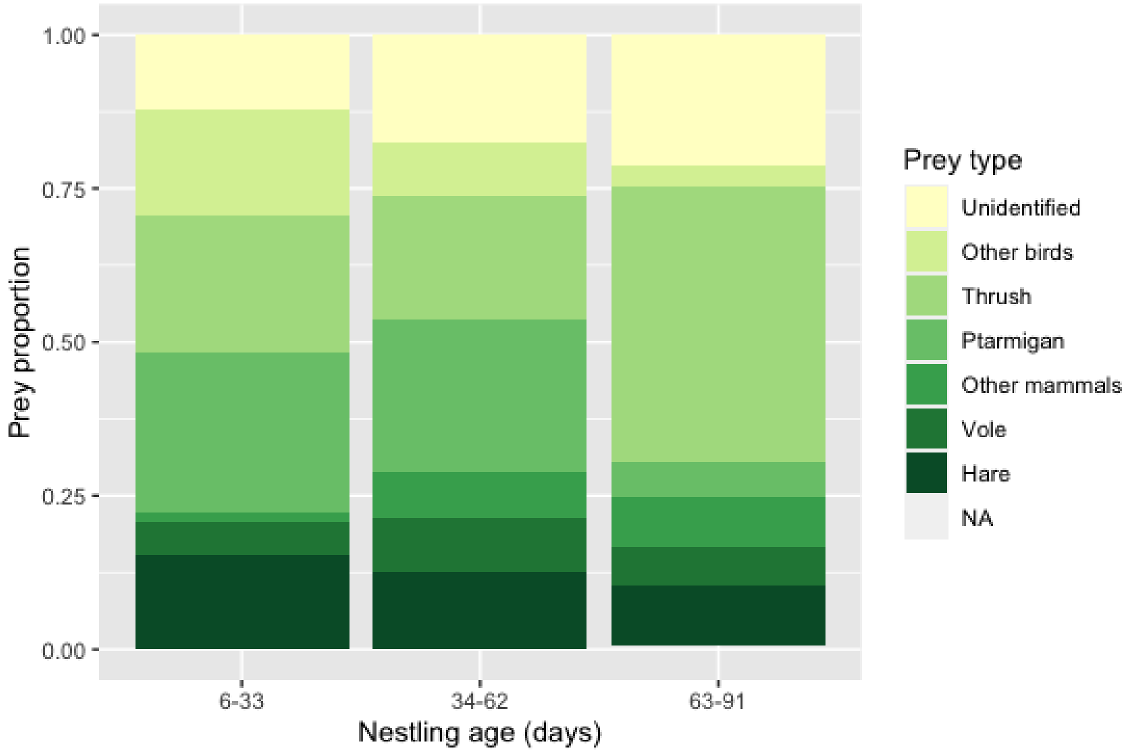

Figure 1. Proportion of prey from the major prey types. The nestling age is divided into three age groups.

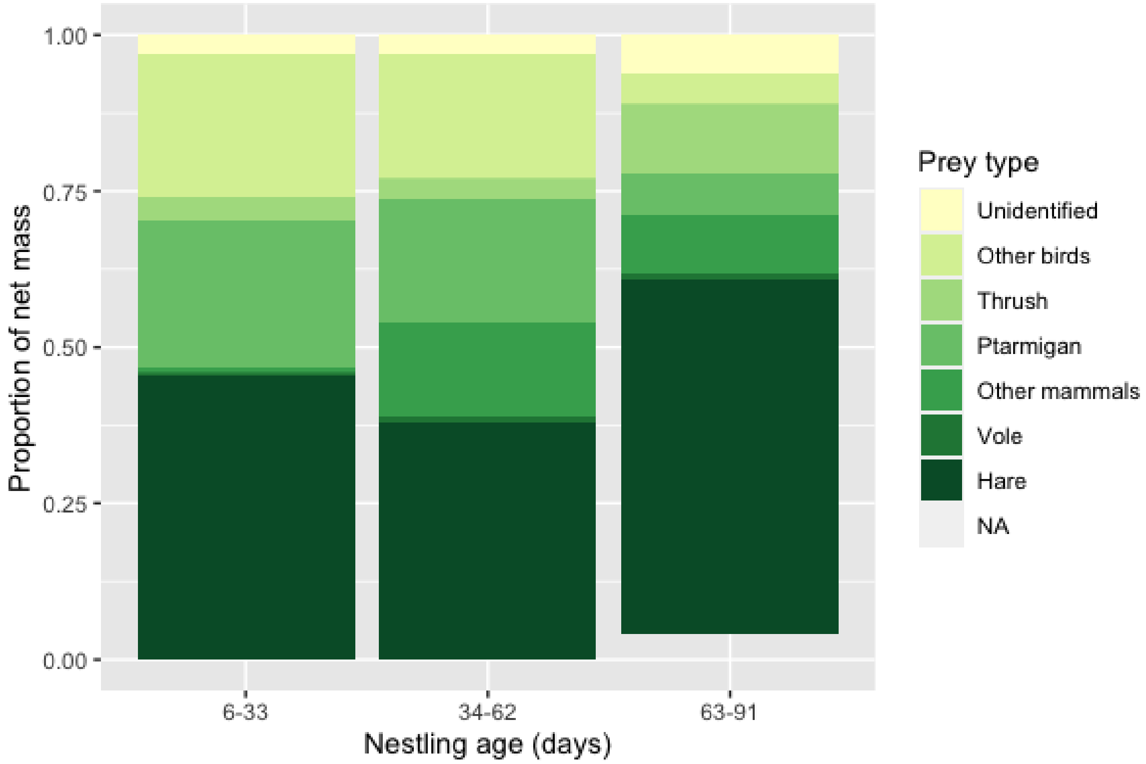

Figure 2. The proportion of net prey mass from major prey types. The nestling age is divided into three age groups.

There was a significant positive relationship between the predicted probability of prey being a thrush and the nestling age (Table 2). As the nestlings grow older the probability of a delivered prey being a thrush increased (figure 3).

Table 2. Parameter estimates of the regression model for the probability of prey delivered at the nest being a thrush.

	Estimate	Std. error	t value	p
(Intercept)	-2.118	0.408	-5.183	< 0.001 ***
Nestling age	0.024	0.006	3.798	< 0.001***

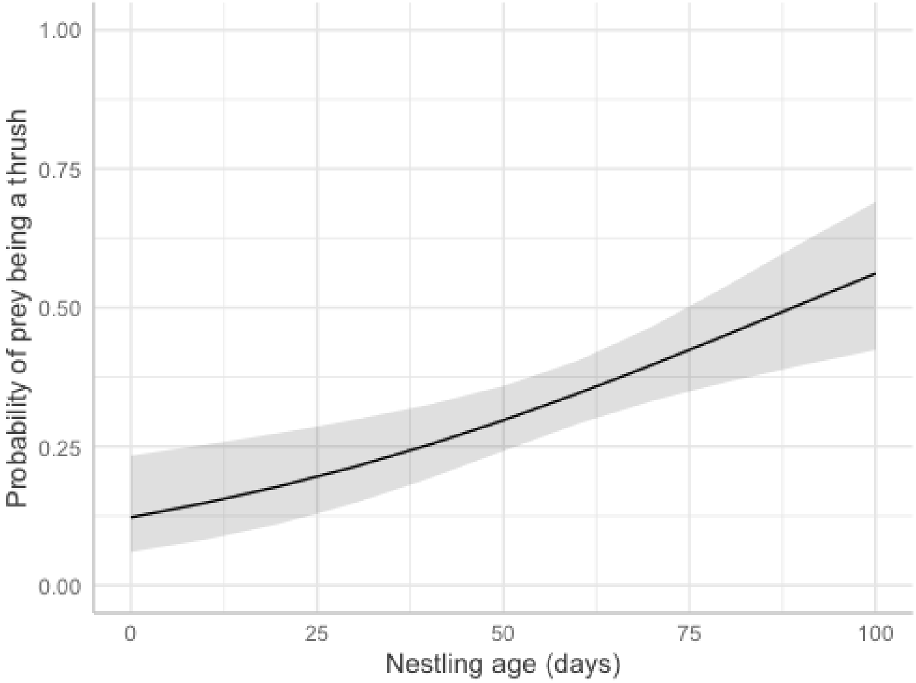

Figure 3. The probability of a delivered prey being a thrush in relation to nestling age, with the black line representing the logistic regression and the grey area the 95% confidence interval.

There was a significant negative relationship between the predicted probability of prey being a ptarmigan and the nestling age (Table 3). As the nestlings grew older the probability of delivered prey being a ptarmigan decreased (Figure 4).

Table 3. Parameter estimates of the regression model for the probability of a prey delivered at the nest being a ptarmigan.

	Estimate	Std. error	t value	p
(Intercept)	-0.058	0.392	-0.149	0.881
Nestling age	-0.033	0.007	-4.286	< 0.001 ***

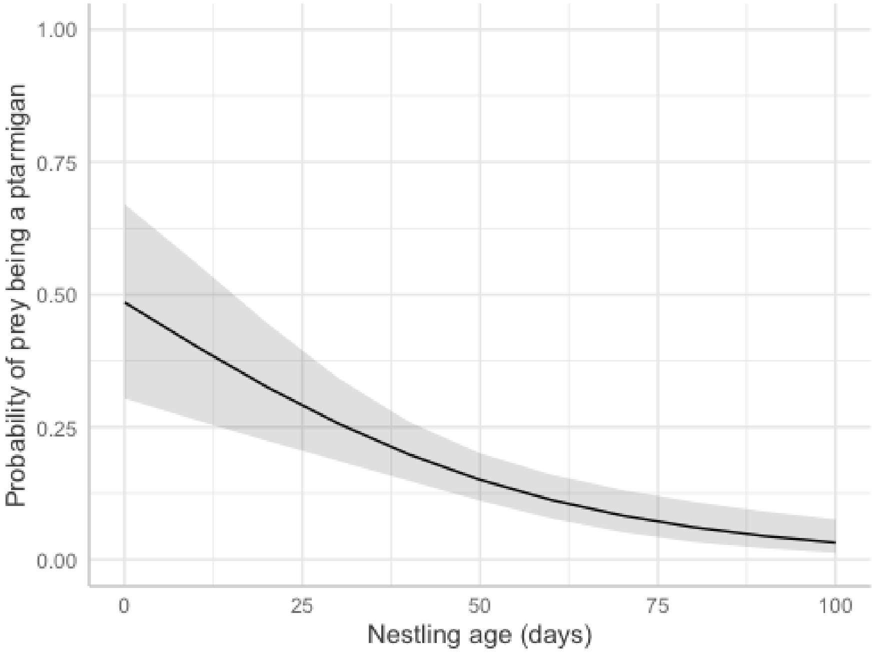

Figure 4. The probability of a delivered prey being a ptarmigan in relation to nestling age, with the black line representing the logistic regression and the grey area the 95% confidence interval.

There was not a significant relationship between the predicted probability of prey being a hare and nestling age (Table 4). There was a tendency for the probability of hare deliveries decreasing with nestling age, but the relationship was not significant (Table 4, Figure 5).

Table 4. Parameter estimates of the regression model for the probability of a prey delivered at the nest being a hare.

	Estimate	Std. error	t value	p
(Intercept)	-1.811	0.489	-3.697	<0.001 ***
Nestling age	-0.003	0.008	-0.465	0.641

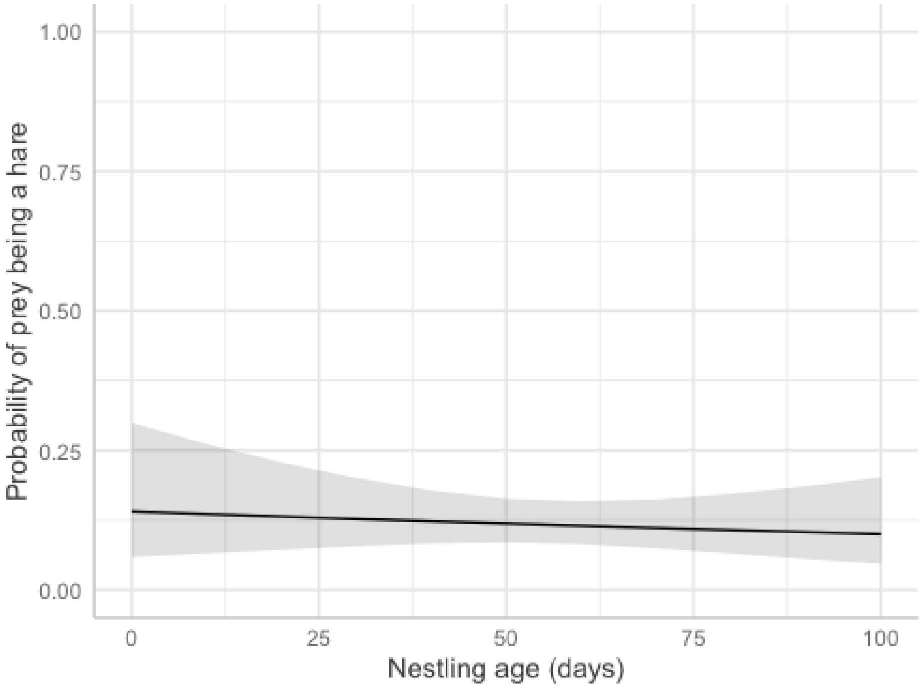

Figure 5. The probability of a delivered prey being a hare in relation to nestling age, with the black line representing the logistic regression and the grey area the 95% confidence interval.

Diel delivery pattern

Prey deliveries were registered in 22 of the 24 hour-blocks of the day. There was no recorded delivery in the hours 01-02 AM and 02-03 AM. The latest prey delivery was recorded at 00:13 because the solar midnight is around 01:15 in the study area during summer. The earliest prey delivery was recorded at 03:41. The best fitting model was model 2 (Table 5), which was selected for further analysis and presented in Appendix A. The diel pattern from the best fitting model is compared to the MESOR, the midline estimating statistic of rhythm. When the lowest 95% confidence interval is above or below the MESOR line, the delivery pattern is significantly different than randomly expected. From around 07 hours until around 18 hours the delivery rate was significantly higher than what can be randomly expected. From 21 hours until 05 hours the prey delivery rate was significantly lower than randomly expected (Figure 6). In the morning from 08 hours until 11 hours there was a peak in prey delivery rate. After 12 hours the rate decreased until a new smaller peak in delivery from 16 hours until 18 hours. After this last peak the delivery rate decreased further and remained low until the first peak the next morning.

Table 5. Parameter estimates for the best fitting regression model (model 2 in Appendix A) predicting the probability of a prey item being delivered at the nest throughout the day.

	Estimate	Std. error	z value	p
(Intercept)	-2.641	0.099	-26.504	< 0.001 ***
I(cos(2 * pi * Hour/24))	-1.349	0.152	-8.828	< 0.001 ***
I(sin(2 * pi * Hour/24))	-0.272	0.111	-2.438	0.014 *
I(cos(2 * 2 * pi * Hour/24))	-0.397	0.116	-3.409	0.0006 ***
I(sin(2 * 2 * pi * Hour/24))	-0.422	0.114	-3.602	0.0003 ***

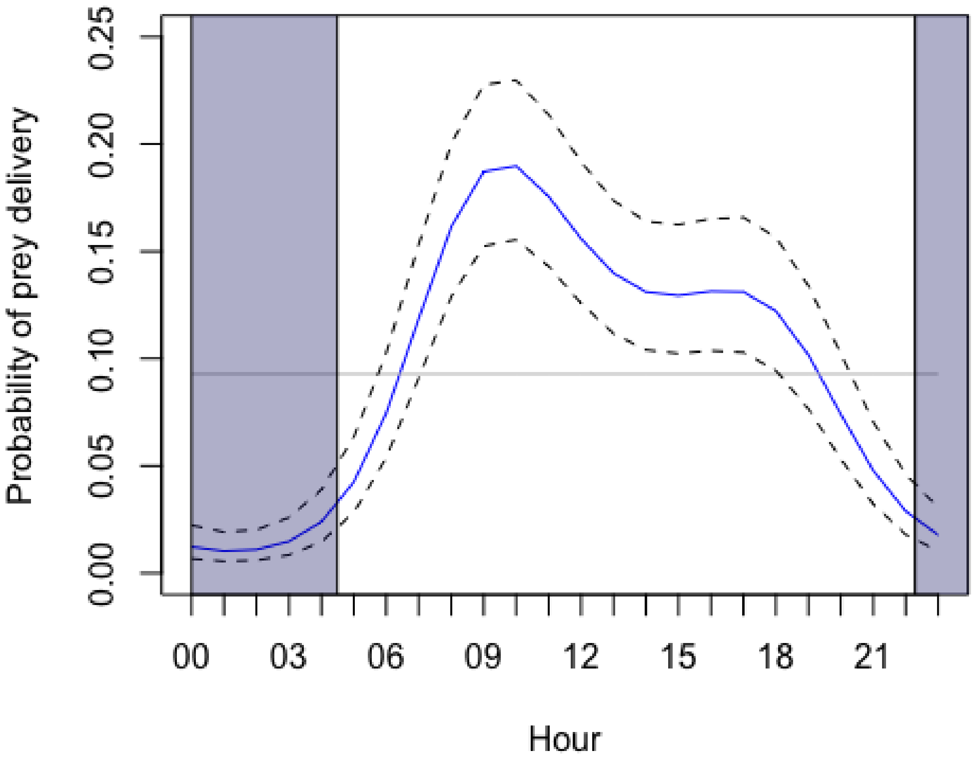

Figure 6. The probability of at least one prey being delivered in each hour block at the golden eagle nest is represented by the blue line. The dashed black lines represent the 95% confidence interval. The vertical grey line represents the midline estimating statistic of rhythm MESOR, and the blue boxes on either side represent the hours between sunset and sunrise in Norwegian summertime, at the study site during the average day of the study.

The diel delivery pattern was also explored for mammalian prey species, the best fitting model was selected using AIC, and model 1 was used for further testing, candidate models are presented in Appendix B. Mammalian delivery only had one peak, which was much lower than in the plot containing all prey species. The delivery rate of mammalian prey was significantly higher than randomly expected from 07 hours until 13 hours, and significantly lower than randomly expected from 20 hours until 04 hours (Figure 7).

Table 6. Parameter estimates for the best fitting regression model (model 1 in Appendix B) predicting the probability of a mammalian prey item being delivered at the nest throughout the day.

	Estimate	Std. error	z value	p
(Intercept)	-3.927	0.165	-23.734	< 0.001 ***
I(cos(2 * pi * Hour/24))	-1.176	0.216	-5.431	< 0.001 ***
I(sin(2 * pi * Hour/24))	0.39	0.190	2.083	0.037 *

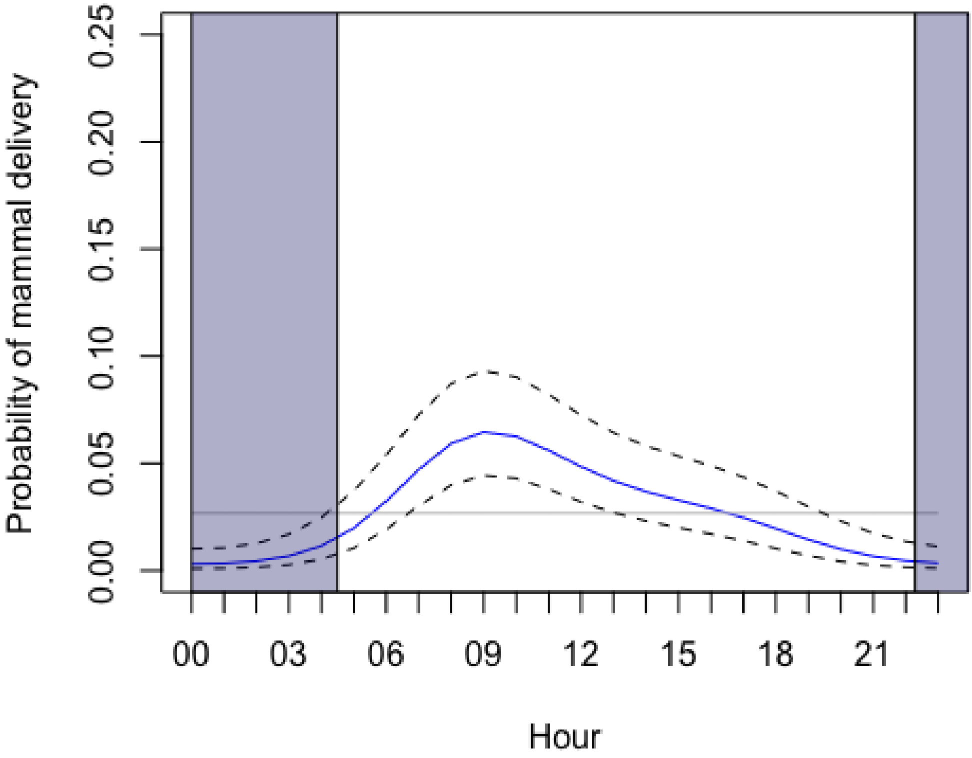

Figure 7. The probability of at least one mammalian prey being delivered at the golden eagle nest in each hour block is represented by the blue line. The dashed black lines represent the 95% confidence interval. The vertical grey line represents the midline estimating statistic of rhythm MESOR, and the blue boxes on either side represent the hours between sunset and sunrise in Norwegian summertime, at the study site during the average day of the study.

For avian prey the delivery pattern was one wide peak, reminiscent of a drawn-out bell curve. The best fitting model was selected using AIC, and model 2 was used for further testing, and is presented in Appendix A. The delivery rate was significantly higher randomly expected from 07 hours until 18 hours, and significantly lower than randomly expected from 21 hours until 05 hours (Figure 8). There was a tendency towards three smaller peaks in the delivery pattern, one in the morning from around 08 hours until 10 hours, one during the afternoon from 12 hours until 15 hours, and the last peak in the evening from 18 hours until 20 hours. However, the last peak was not higher than what could be randomly expected, as the lower confidence interval was under the MESOR line.

Table 7. Parameter estimates for the best fitting regression model (model 2 in Appendix A) predicting the probability of an avian prey item being delivered at the nest throughout the day.

	Estimate	Std. error	t value	p
(Intercept)	-3.142	0.133	-23.504	< 0.001 ***
I(cos(2 * pi * Hour/24))	-1.499	0.204	-7.349	< 0.001 ***
I(sin(2 * pi * Hour/24))	-0.483	0.141	-3.416	< 0.001 ***
I(cos(2 * 2 * pi * Hour/24))	-0.473	0.144	-3.273	0.001 **
I(sin(2 * 2 * pi * Hour/24))	-0.459	0.142	-3.232	0.001 **

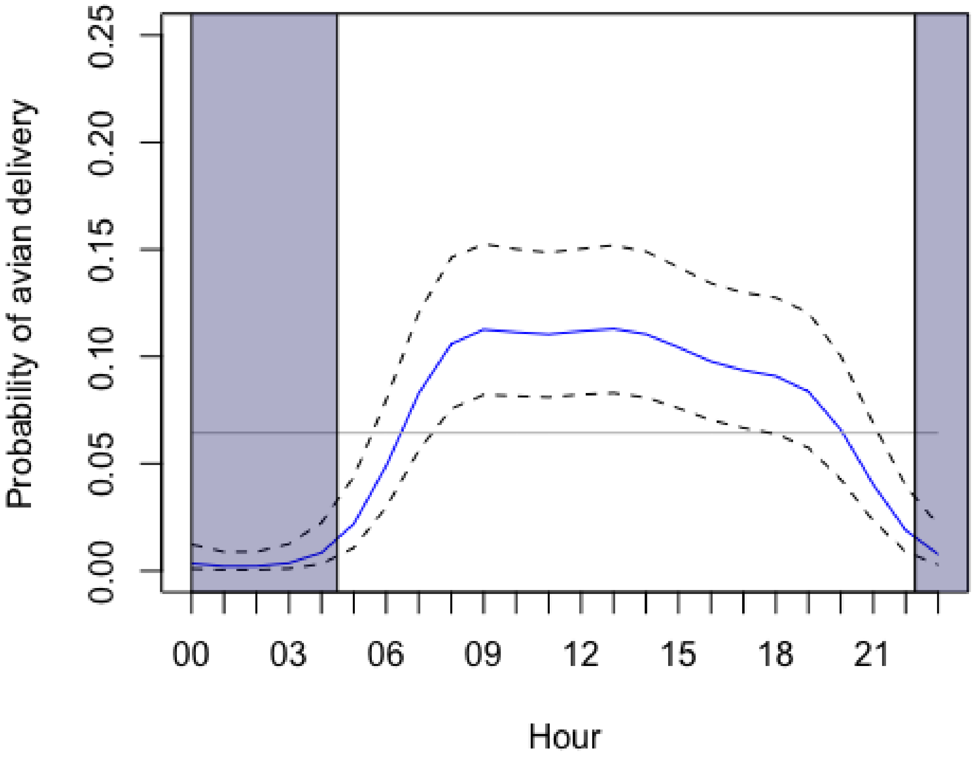

Figure 8. The probability of at least one avian prey being delivered at the golden eagle nest in each hour block is represented by the blue line. The dashed black lines represent the 95% confidence interval. The vertical grey line represents the midline estimating statistic of rhythm MESOR, and the blue boxes on either side represent the hours between sunset and sunrise in Norwegian summertime, at the study site during the average day of the study.

Activity pattern and overlap

The activity distribution plots were divided according to prey class, with mammals and birds in separate plots. Mammals in general had a lower frequency of delivery, and an earlier main peak in activity distribution, compared to birds. The first and main activity peak in the mammal group was in the morning from around 09 hours until 12 hours (Figure 9). With a tendency to a second peak in the evening around 18 hours.

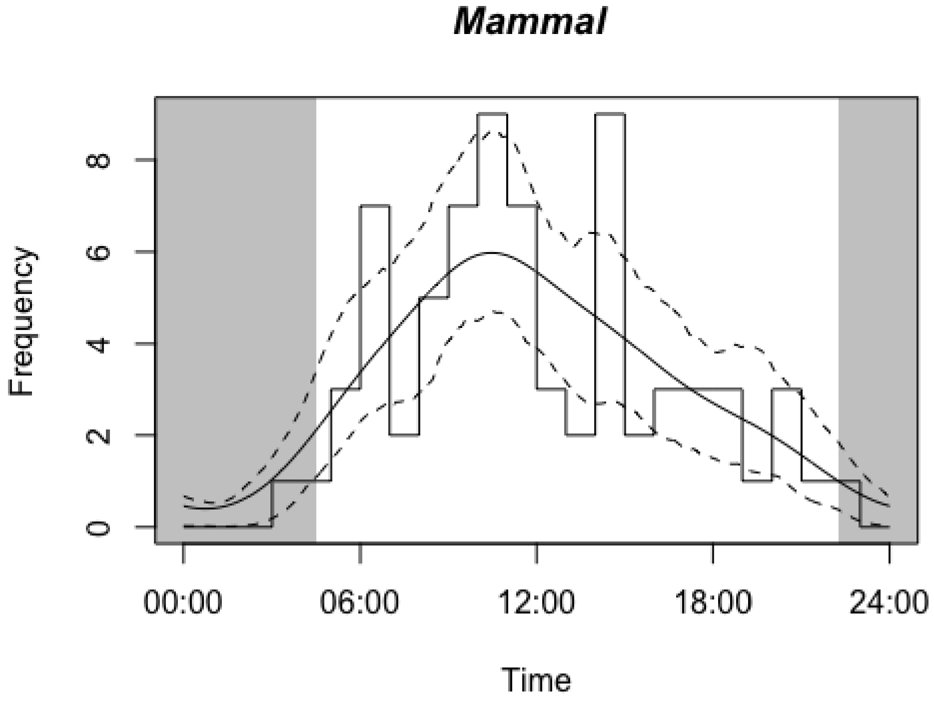

Figure 9. Activity distribution plot for deliveries of mammals at the golden eagle nest. Predicted frequency of mammal prey delivery in relation to time of day during the nesting season. The predicted frequency is represented by the black line and the 95% confidence interval is represented by the dashed black lines. The bars represent actual number of mammalian prey delivered in each hour block, and the grey squares on either side represent the hours between sunrise and sunset for Norwegian summertime, at the study site during the average day of the study.

Avian prey had a higher delivery frequency, and the activity distribution peak was later in the day, compared to mammalian prey. The activity distribution for avian prey peaked around midday, with a peak ranging from around 10 hours until 14 hours (Figure 10).

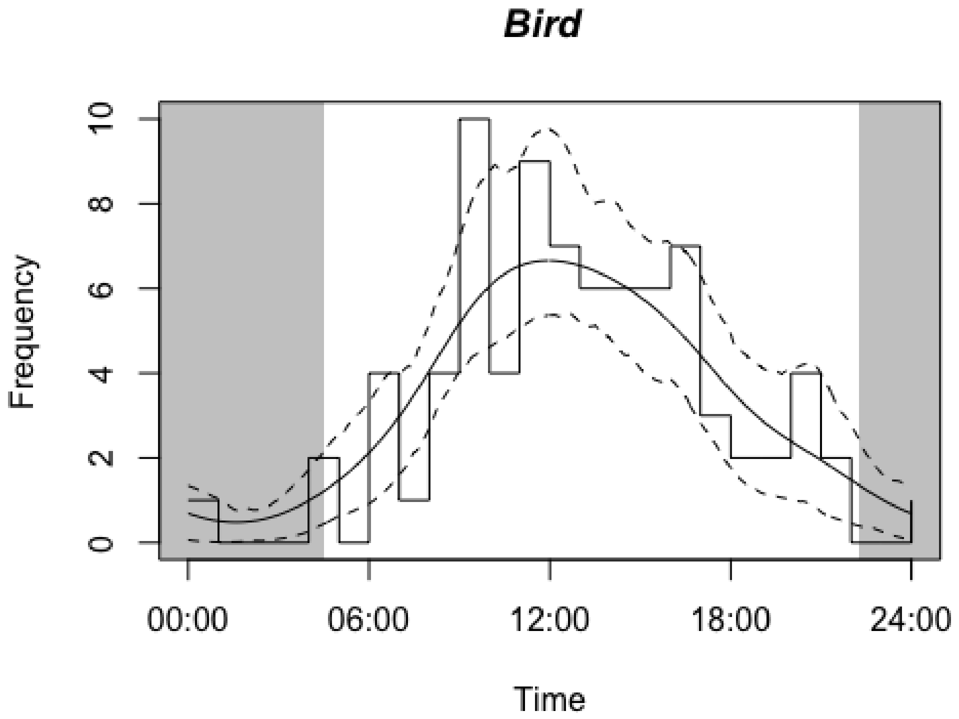

Figure 10. Activity distribution plot for deliveries of birds at the golden eagle nest. Predicted frequency of avian prey delivery in relation to time of day during the nesting season. The predicted frequency is represented by the black line and the 95% confidence interval is represented by the dashed black lines. The bars represent actual number of avian prey delivered in each hour block, and the grey squares on either side represent the mean hours between sunrise and sunset for Norwegian summertime, at the study site during the average day of the study.

The overlap coefficient between the kernel density of thrushes and voles as prey species was Δ = 0.855 (Table 8). And the precision of the coefficient of overlap was estimated by the bootstrapped mean overlap, which is 0.765. Thrushes had a higher delivery rate than voles, with one peak in deliveries around midday from 12 hours until 15 hours (Figure 11). Voles had a lower delivery rate with a split delivery distribution of two separate peaks, one in the morning from 07 hours until 10 hours, and one lower peak in the evening from 18 hours until 20 hours (Figure 11).

Table 8. Estimated overlap between thrushes and voles, using estimator Δ 1 (Delta hat 1). Activity densities were estimated by kernel density, and precision was checked by the bootstrapped mean overlap.

Species	Overlap coefficient Δ	Bootstrap mean overlap	Bootstrap confidence interval (basic0)	
			Lower	Upper
Thrush and vole	0.855	0.765	0.690	0.986

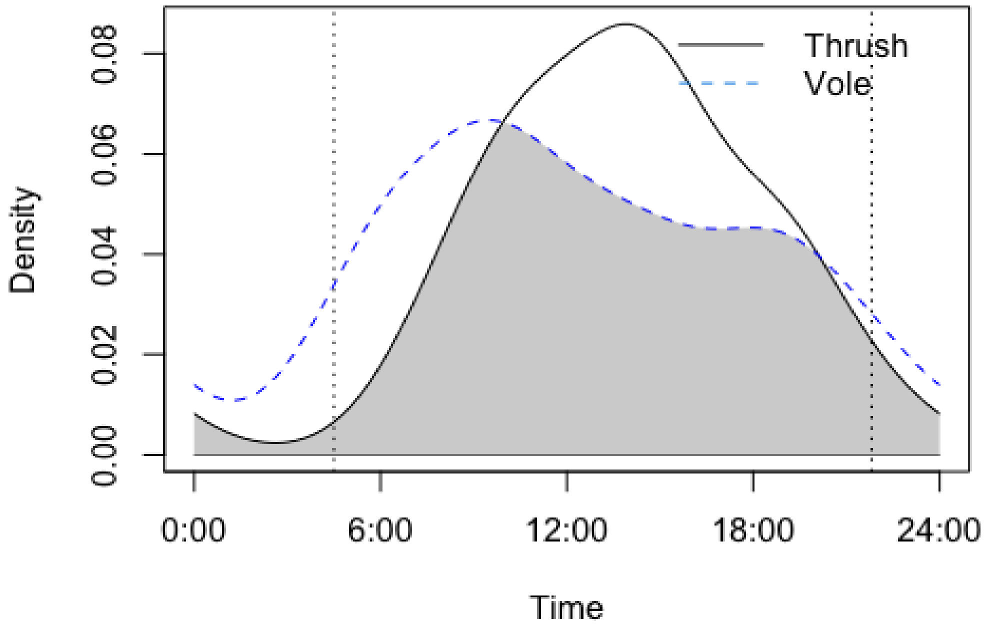

Figure 11. The overlap of delivery density between thrushes and voles. The black solid line represents the density of thrush deliveries in relation to hour of the day. The blue dashed line represents the density of vole deliveries in relation to hour of the day. The grey area under the minimum of the two density estimates is the overlap coefficient (Δ). The two black vertical dashed lines represent the area between sunset and sunrise for Norwegian summertime at the study site during the average day of the study.

The delivery pattern of hares followed a similar distribution to that of voles. However, the hare delivery distribution had a much higher initial peak, with a higher density of deliveries from 07 hours until around 10 hours. As for the voles, the hare delivery had a second, much lower peak around 17 hours until 20 hours, after a steep decline in deliveries from the initial peak (Figure 12). This creates an area around midday where there is little overlap in the delivery density of hares and thrushes, as thrushes had their main peak in delivery density slightly after midday.

The overlap coefficient between the kernel density of thrushes and voles as prey species was Δ = 0.734 (Table 9). And the precision of the coefficient of overlap was estimated by the bootstrapped mean overlap, which is 0.716 (Table 9). The overlap coefficient of thrush and hare is lower than that of thrushes and voles.

Table 9. Estimated overlap between thrushes and hares, using estimator Δ 1 (Delta hat 1). Activity densities were estimated by kernel density, and precision was checked by the bootstrapped mean overlap.

Species	Overlap coefficient Δ	Bootstrap mean overlap	Bootstrap confidence interval (basic0)	
			Lower	Upper
Thrush and hare	0.734	0.716	0.588	0.863

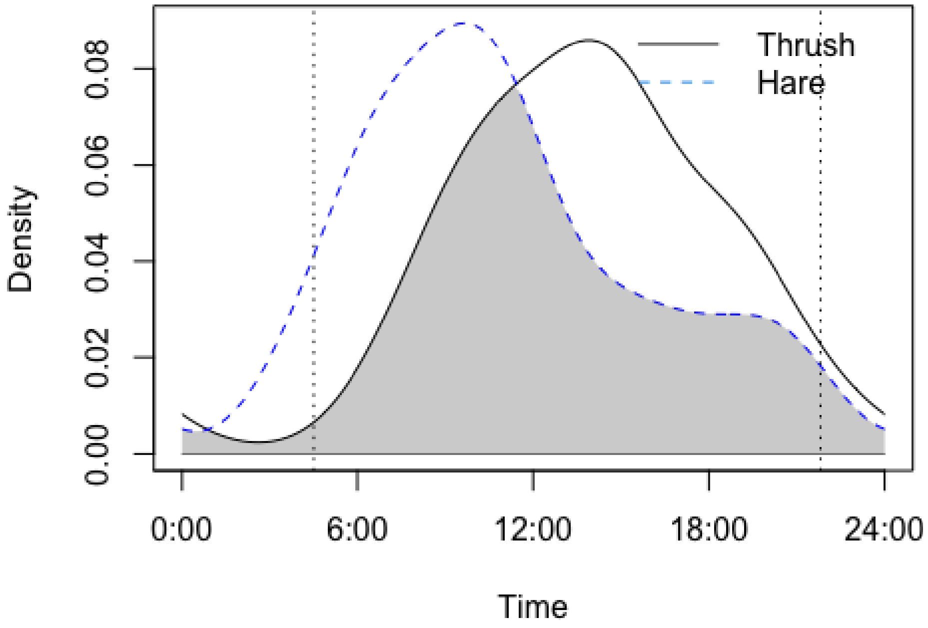

Figure 12. The overlap of delivery density between thrushes and hares. The black solid line represents the density of thrush deliveries in relation to hour of the day. The blue dashed line represents the density of hare deliveries in relation to hour of the day. The grey area under the minimum of the two density estimates is the overlap coefficient (Δ). The two black vertical dashed lines represent the area between sunset and sunrise for Norwegian summertime at the study site during the average day of the study.

There was a larger overlap in delivery densities between mammals and birds. But with separate peaks which did not overlap, with mammalian delivery having a peak slightly before midday from 08 hours until 10 hours, and avian prey delivery having one peak from 09 hours until 11 hours and one slightly higher peak in deliveries from 13 hours until 15 hours (Figure 13). When all prey from each taxonomic group were combined the range of both prey densities became wider, also creating a larger time frame with overlap. The overlap coefficient between the kernel density of mammalian and avian prey species was Δ = 0.861 (Table 10). And the precision of the coefficient of overlap was estimated by the bootstrapped mean overlap, which is 0.838.

Table 10. Estimated overlap between mammals and birds, using estimator Δ 4 (Delta hat 4). Activity densities were estimated by kernel density, and precision was checked by the bootstrapped mean overlap.

Species	Overlap coefficient Δ	Bootstrap mean overlap	Bootstrap confidence interval (basic0)	
			Lower	Upper
Mammal and bird	0.861	0.838	0.742	0.922

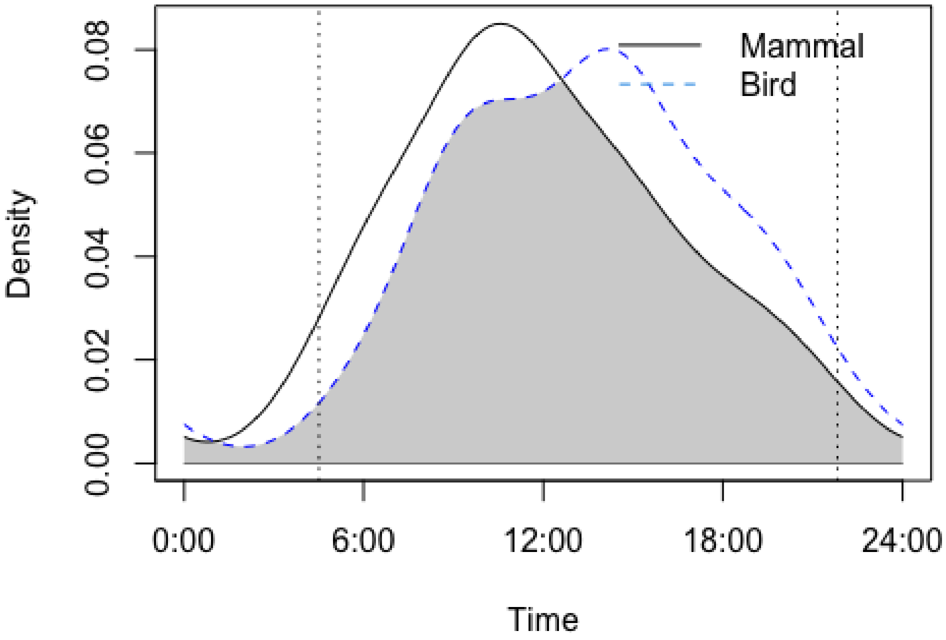

Figure 13. The overlap off delivery density between mammalian and avian prey. The black solid line represents the density of mammal deliveries in relation to hour of the day. The blue dashed line represents the density of avian deliveries in relation to hour of the day. The grey area under the minimum of the two density estimates is the overlap coefficient (Δ). The two black vertical dashed lines represent the area between sunset and sunrise for Norwegian summertime at the study site during the average day of the study.

Effect of nestling age

Nestling age affected the number of prey deliveries per day significantly (Table 11). The predicted number of prey items delivered at the nest increased as the nestlings grew older, until a few days before fledging when the number of prey items decreased (Figure 14). The highest number of prey deliveries in one day was 12, and occurred when the nestlings were 69 days old. There were 10 days when the parents did not deliver any prey, or no prey was recorded due to technical difficulties.

Table 11. Parameter estimates of the regression model prediction number of prey delivered at the golden eagle nest each day.

	Estimate	Std. error	t value	p
Intercept	1.97854	0.66369	2.981	0.00392 **
Nestling age	0.03649	0.01183	3.084	0.00289 **

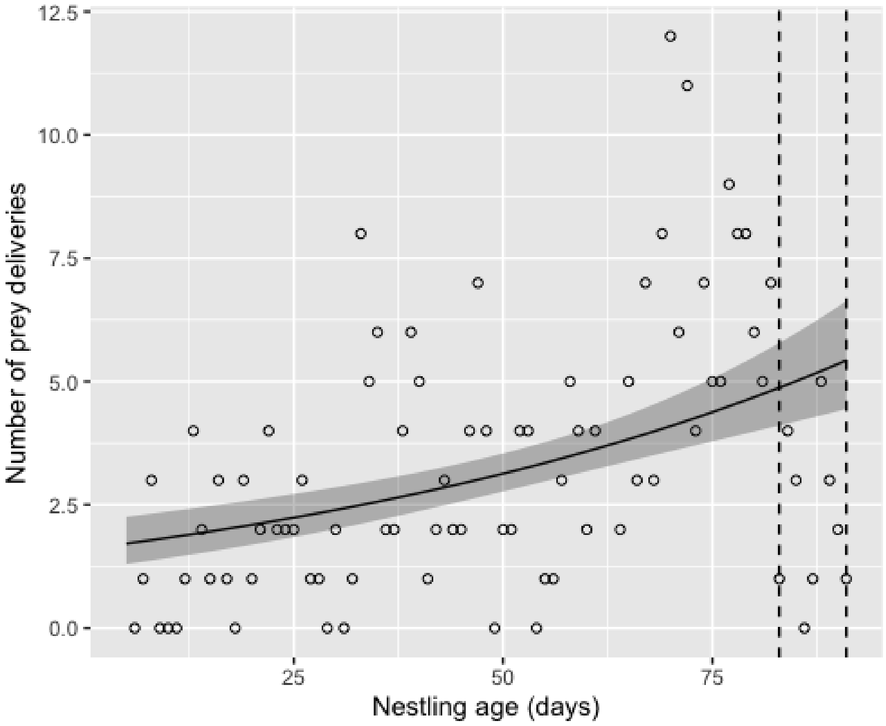

Figure 14. The number of prey items delivered at the golden eagle nest each day in relation to nestling age. The black line represents the predicted number of deliveries per day from the Poisson regression in table 11. The gray area around the line is the 95% confidence interval. The two vertical dashed lines represent at what ages the two golden eagle nestlings fledged.

While there was an increase in number of prey items delivered per day in relation to nestling age, the net prey mass delivered per day was not significantly affected by nestling age (Table 12). There was no significant predicted increase or decrease in total net mass delivered per day in relation to nestling age. There was a tendency to a positive trend for delivered net prey mass in relation to nestling age, but the relationship was not significant (Figure 15).

Table 12. Parameter estimates of the regression model predicting net prey mass delivered at the golden eagle nest each day.

	Estimate	Std. error	t value	p
Intercept	930.943	356.571	2.611	0.0107 *
Nestling age	9.661	6.486	1.489	0.1401

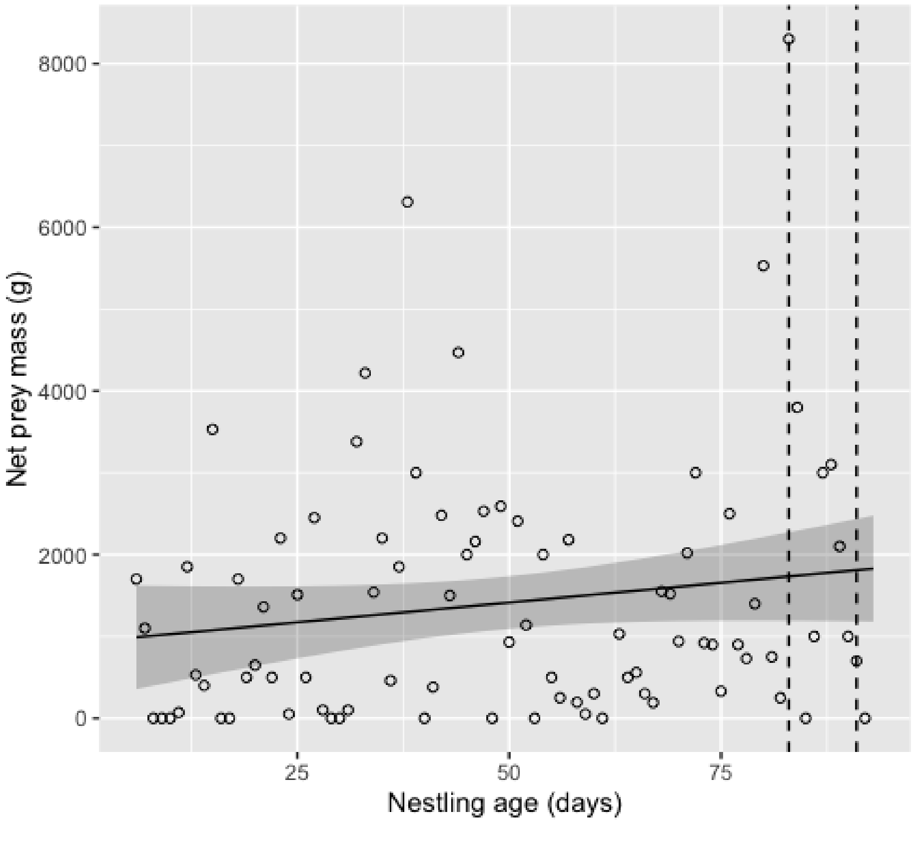

Figure 15. Total net prey mass delivered at the golden eagle nest per day in relation to nestling age. The black line represents the predicted net mass delivered each day from the linear regression in table 12. The gray area around the line is the 95% confidence interval. The two vertical dashed lines represent at what ages the two golden eagle nestlings fledged.

The gross prey mass of prey delivered at the nest was best explained by a model containing nestling age, delivering sex, and the interaction between nestling age and delivering sex.

Table 13. AIC model selection with the different candidate models for the effect of gross prey mass for prey items delivered per day.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
2	Nestling age * Delivering sex	5	855.86	0.00	0.91
1	Nestling age + Delivering sex	4	860.45	4.59	0.09
3	Delivery sex	3	868.39	12.53	0.00
4	Delivering sex	3	872.78	16.92	0.00
0	Intercept	2	879.38	23.53	0.00

The only significant effect was that of the interaction between nestling age and the delivery parent being the male, which was negative (Table 14). The male had a predicted probability of delivering prey with a lower gross body mass than the female as the nestlings grew older. The female tended to deliver prey with a larger gross prey mass which increased with nestling age, however, this relationship was not significant. The data for gross prey mass was log-transformed to simulate normally distributed data for this analysis (Figure 16).

Table 14. Parameter estimates of the best fitting model of (model 2, table 13), which contained the variables affecting gross mass of prey items delivered at the nest.

	Estimate	Std. error	z value	p
(Intercept)	5.338	0.518	10.288	< 0.001 ***
Nestling age	0.005	0.008	0.694	0.488
Delivery sex Male	1.084	0.569	1.905	0.057 .
Nestling age: Delivering sex Male	-0.023	0.009	-2.579	0.010 *

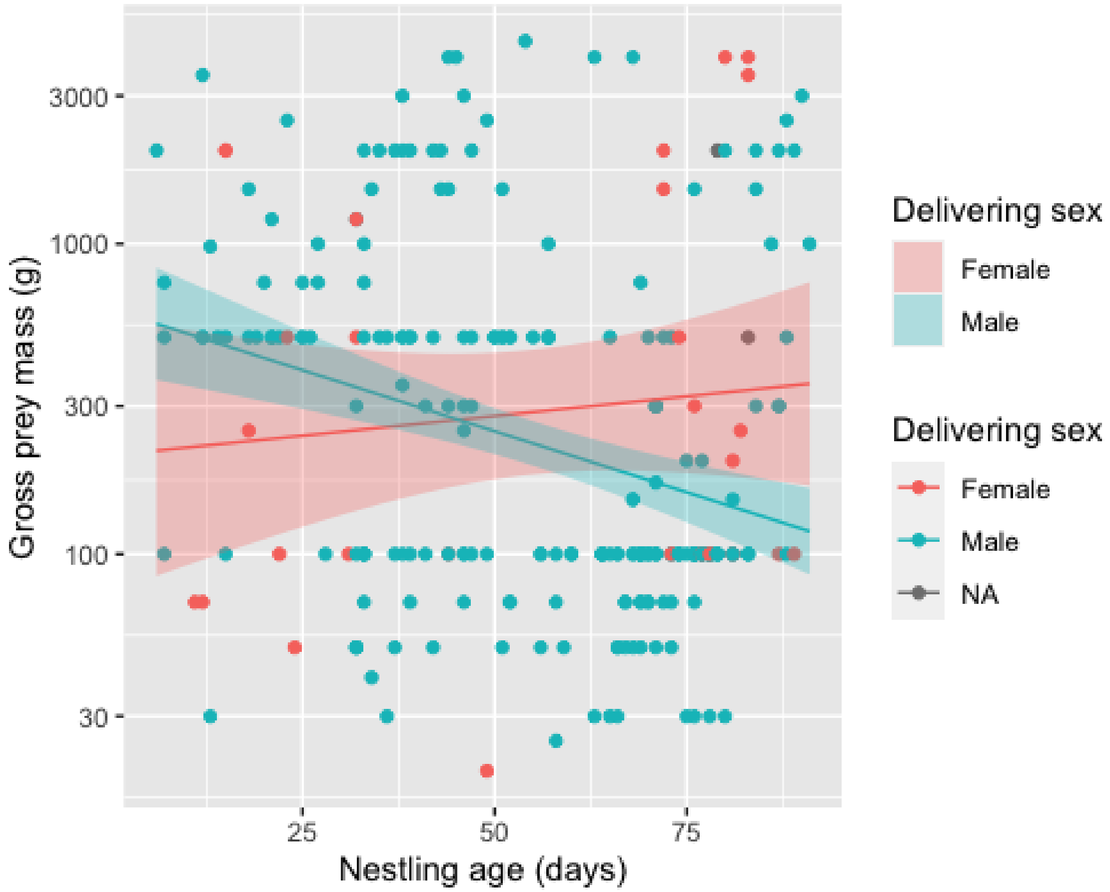

Figure 16. Gross prey mass for prey items delivered per prey in relation to nestling age, for prey items delivered by the male (blue) and female (red). The red and blue lines represent linear regression prediction of gross mass for each delivery parent. The colored areas represent the 95% confidence interval for each colored line.

Prey handling

The first instance when a nestling fed unassisted was at 32 days age when the male parent delivered an entire thrush nest, containing three nestlings. The eagle nestling swallowed two thrush nestlings whole without assistance and was fed the third in pieces. The prey item was so small that there was no handling prior to swallowing. The first time a nestling both handled and ingested a prey unassisted was at the age of 56 days when one nestling dismembered a vole before ingesting it.

Any prey handling done prior to delivery at the nest was registered as the prey condition. Out of the 283 recorded prey items, the prey condition at delivery could be determined for 259. For these prey 15.8% were decapitated prior to delivery at the nest, and 18.0% were partially eaten prior to delivery. When dividing prey into classes, birds 17.0% were decapitated, 12.0% were partially eaten, and 18.0% were plucked prior to delivery at the nest. For mammals 0.8% were decapitated and 28.0% were partially eaten prior to delivery.

The most important variable when assessing prey handling was nestling age. As the nestlings grew older, they received less help from parents with plucking, partitioning, and handling prey. In the later stages of the nestling period (63-91 days), nestlings were observed on several occasions chasing the delivering parent off the nest after the prey was delivered (Personal observation.).

The variables affecting the probability of a prey being delivered decapitated were the nestlings' age and the gross body mass of the prey. Out of the 259 prey items where handling could be determined, 41 (15.8%) prey were decapitated prior to delivery at the nest. The remaining 218 prey were either eaten at, plucked, or intact. Variables that may affect the probability of prey being decapitated prior to delivery are nestling age, the delivering sex, and gross prey mass. Based on AIC model 2 was determined to be the best fitting model and used for further testing (Table 15). Model 2 contained nestling age and the gross prey body mass.

Table 15. AIC analysis with the different candidate models for the effect on the probability of prey being delivered decapitated.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
2	Nestling age + Gross body mass	3	207.05	0.00	0.67
1	Nestling age * Gross body mass	4	208.73	1.69	0.29
6	Nestling age + Delivering sex	3	214.11	7.06	0.02
5	Nestling age * Delivering sex	4	214.53	7.48	0.02
4	Nestling age	2	215.29	8.24	0.01
3	Gross body mass	2	224.49	17.44	0.00
0	Intercept	1	236.18	29.13	0.00

The probability that a prey item was delivered decapitated decreased significantly with nestling age and there was not a significant relationship between gross prey mass and the probability of decapitation (Table 15, Figure 17). The highest probability of a prey being decapitated prior to delivery was found when the nestling age was low, and the gross prey mass was high (Figure 17).

Table 16. Estimates of the best fitting logistic regression (model 2 in table 15) predicting the probability of prey being decapitated prior to delivery at the nest. variables

	Estimate	Std. error	z value	p
Intercept	-0.118	0.431	-0.274	0.784
Nestling age	-0.034	0.008	-4.218	< 0.001 ***
Gross body mass	0.00019	0.00018	1.062	0.288

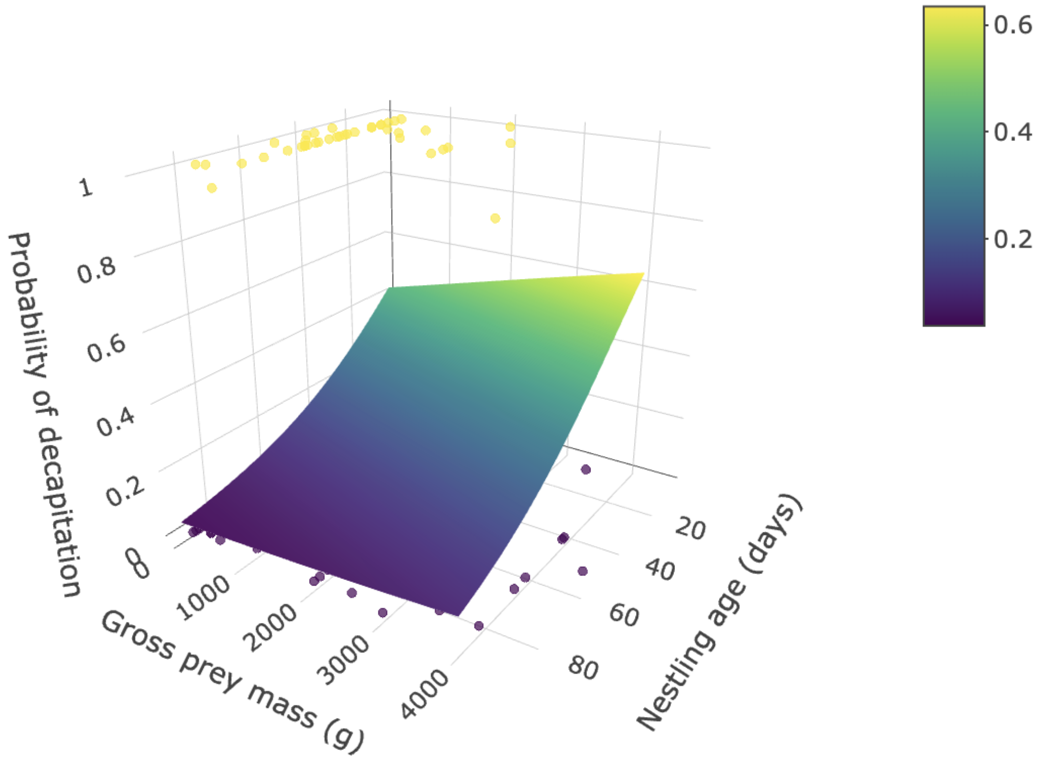

Figure 17. Predicted probability of prey being decapitated prior to delivery at the nest, relative to nestling age (days) and the gross body mass (g) of the prey. The 3D plane is colored after the predicted probability of a prey item being decapitated prior to delivery at the nest.

Whether nestlings were feeding with no help from parents was affected by the model containing nestling age and the net body mass of the prey item (Table 17). As the nestlings grew older, they handled a larger portion of the prey themselves, and the probability of unassisted feeding increased significantly with the age of the nestlings, and the probability of unassisted feeding decreased significantly with the net body mass of the prey (Table 18). Larger prey was at least partly handled by the parents in most cases, with the nestlings being able to handle larger prey as they grew older. The highest probability of an unassisted feeding was found when the nestling age was high, and the gross prey mass was low (Figure 18).

Table 17. The model selection of AIC, used to identify the logistic regression models whose variables most accurately predicted the probability of nestlings handling prey unassisted.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
2	Nestling age + Net body mass	3	127.55	0.00	0.73
1	Nestling age * Net body mass	4	129.50	1.95	0.27
3	Nestling age	2	234.46	106.90	0.00
4	Net body mass	2	265.02	137.47	0.00
0	Intercept	1	381.94	254.39	0.00

The probability of unassisted feeding increased significantly with nestling age, and the probability of unassisted feeding decreased significantly with the net body mass of the delivered prey item (Table 18).

Table 18. Parameter estimates of the best fitting logistic regression (model 2 in table 17) predicting the probability of nestlings handling prey unassisted.

	Estimate	Std. error	z value	p
Intercept	-9.252	1.593	-5.807	< 0.001 ***
Nestling age	0.163	0.024	6.593	< 0.001 ***
Net body mass	-0.007	0.001	-4.869	< 0.001 ***

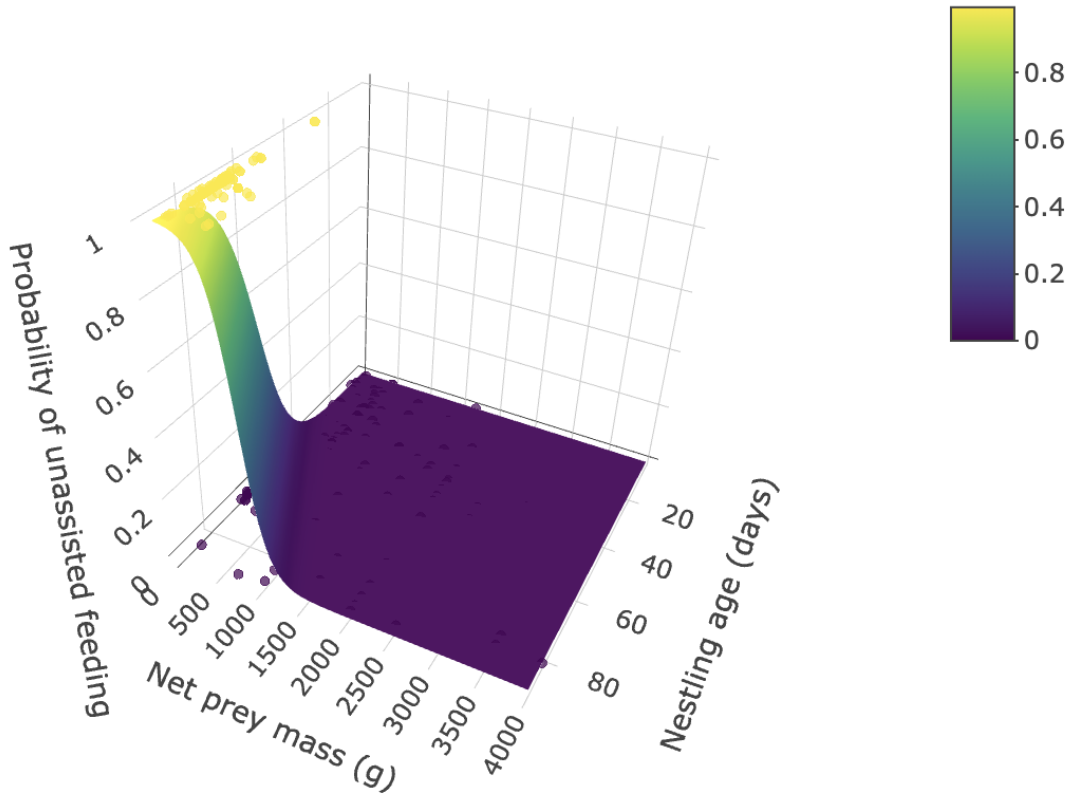

Figure 18. The predicted probability of a nestling feeding unassisted in relation to the nestling age (days) and the net body mass (g) of the prey. The 3D plane is colored after the predicted probability of unassisted feeding.

The probability of unassisted feeding was around 50% when the nestlings were 58 days old for the smallest prey items with a net mass of 20 g. While the probability of unassisted feeding was around 50% when the nestlings were 78 days old when considering the mean net prey mass of 487 g (Table 19). Predictions were preformed using model 2 presented in Table 17.

Table 19. Predicted probability of nestlings feeding unassisted for nestling age, and the minimum net prey mass (20 g) and mean net prey mass (487 g).

Nestling age (days)	Net body mass (g)	Predicted fit	Upper fit	Lower fit
58	20	0.522	0.676	0.332
78	487	0.520	0.733	0.300

Variables influencing whether avian prey was plucked prior to delivery were explored using AIC and presented in Appendix C. Only avian prey was included as they are the only relevant prey class. The best fitting model was model 7 which includes gross prey mass. There was not a significant relationship between the probability of an avian prey being plucked prior to delivery and the gross prey mass (Table 20).

Table 20. Parameter estimates of the best fitting logistic regression predicting the probability of an avian prey being plucked.

	Estimate	Std. error	t value	p
Intercept	-1.6428257	0.2123211	-7.737	< 0.001 ***
Gross body mass	-0.0003568	0.0002703	-1.320	0.187

Discussion

Prey delivered at the nest

The golden eagle pair that I monitored in 2022 delivered 283 prey items to the nest during the 87 days of monitoring. The prey species delivered were 70,3% birds, 26,2% mammals, and 3, 5% prey that could not be determined to a taxonomic group. The total gross mass of prey was 140 273 g, which correlates to a mean gross mass of 495,7 g. Previous video monitoring studies of golden eagles in Norway with two nestlings had 304 prey deliveries (Mjelde, 2021) during 78 days of monitoring, and 181 prey deliveries (Skouen, 2012) during 52 days of monitoring. These studies respectively had a gross mass of 83 747g with a mean of 276g, and a gross mass of 89 260g with a mean of 493g. Other studies with only one nestling has recorded 72 prey deliveries (Nygård, 2015) during 71 days of monitoring, and 120 prey deliveries (Dihle, 2015) during 82 days of monitoring. They found the mean gross mass per prey to be 441g and 607g, respectively. The study done by (Günther, 2020) used data from four nests with one or two nestlings, recording a total of 456 prey deliveries during around 120 days of monitoring, and a mean gross mass of 66 516g per nest, and a mean prey weight of 737g.

Similarly to previous studies of golden eagle's prey choice in Scandinavia, birds were the most important taxonomic group in terms of prey number in my study (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021). The proportion of avian prey found in the diet in previous video monitoring studies ranges between 34% (Dihle, 2015) and 89% (Mjelde, 2021). However, three of five similar studies show a proportion of avian prey similar to the one found in my study, with 64% (Günther, 2020), 67% (Nygård, 2015), and 70% (Skouen, 2012) avian prey.

Although birds were the most important group in terms of prey number, they did not account for the largest proportion of prey mass, I found that avian prey made up 43.0% of the mean gross mass and mammals accounted for 76.9% of the mean gross mass. The fact that birds were the most important group by number of deliveries, but mammals were most important in terms of prey mass was also found in the previous video monitoring studies in Norway (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021). The importance of avian prey in the golden eagle diet was also found in studies based on prey remains and pellets in both Norway and Sweden (Tjernberg, 1981; Johnsen et al., 2007). While the study done by Högström and Wiss (Hogstrom & Wiss, 1992) also used prey remains and pellets to estimate the golden eagle's diet, they found at least 50% of prey to be mammals. More traditional methods for investigating the diet of raptors has been collecting pellets and prey remains from in and around the nest (Tjernberg, 1981). However, such methods have been found to underestimate the presence of smaller birds in the diet (Selas et al., 2007), and raptors tend to ingest a smaller proportion of larger prey items than of smaller prey items, leaving more remains of larger prey to be found (Slagsvold et al., 2010). Thus, more traditional methods may me biased towards larger prey in the diet and underestimate smaller prey like thrushes. While video monitoring at the nest has its own biases, smaller prey are more accurately represented in the diet (Lewis et al., 2004; Tornberg & Reif, 2007), which might explain the larger proportion of smaller bird species, like thrushes, found in video monitoring studies, than previous studies using more traditional methods.

Thrushes were the most important prey species in my study accounting for 33.2% of deliveries, followed by 14.8% ptarmigans and 11.6% mountain hare. In terms of gross mass there was 47.4% mountain hare, 14.0% ptarmigans and 6.3% thrushes recorded in my study. In previous video monitoring studies, the proportion of thrushes has varied between 15% (Dihle, 2015) and 58% (Mjelde, 2021). However, the gross mass of thrushes in the eagle's diet, recorded by video monitoring, has typically been around 5%, and Mjelde (Mjelde, 2021) recorded the highest proportion of gross mass of thrushes at 19%. All video monitoring studies from Norway, including mine, coincide on the importance of thrushes as a prey species for golden eagles during the breeding season. However, several studies using traditional methods in Scandinavia found that thrushes were close to absent from the golden eagles' breeding diet (Sulkava et al., 1999; Nystrom et al., 2006; Johnsen et al., 2007). The difference in method is likely the cause of these diverging results, as more traditional methods have been proven to underestimate smaller prey species in the diet (Lewis et al., 2004; Tornberg & Reif, 2007).

Ptarmigans were the second most numerous prey, and the importance of ptarmigans has varied between video monitoring studies, with the proportion of ptarmigans as prey ranging from 5.8% to 34.3% (Skouen, 2012; Dihle, 2015). While more using more traditional methods Johnsen (Johnsen et al., 2007), recorded as much as 51% ptarmigans in the golden eagle's diet. The gross mass of ptarmigans found in my study is inside the expected interval found in previous video monitoring studies (Skouen, 2012; Nygård, 2015; Günther, 2020; Mjelde, 2021), with the exception of Dihle (Dihle, 2015), who found the gross mass of ptarmigans to be as low as 5%. Local property management in my study area conduct line transect yearly to estimate populations of game birds. The results are made public in Hønsefuglportalen (Hønsefuglportalen, 2023) and showed a very low density of game birds in the area for 2022, with an estimated 3 individuals per km2. Results from grouse transects one year have been found to be a decent estimate for the number of grouse in the golden eagle's diet the same year (Watson, 2010). Contrarily, I found a proportion of ptarmigans in the breeding diet within the range of previous video-monitoring studies. The low population density of ptarmigans in the study area did not appear to have a seriously adverse effect on the proportion of ptarmigans in the diet. This corresponds with other video monitoring studies in Norway which have not found a relationship between estimated ptarmigan populations in the study area, and the proportion of ptarmigans found in the golden eagle's diet (Skouen, 2012; Dihle, 2015; Nygård, 2015; Mjelde, 2021). While Günther (Günther, 2020) did find a relationship between the estimated ptarmigan population and the proportion of ptarmigans in the diet, with a high estimated ptarmigan population density of 12 ptarmigans per km2, and a correspondingly high proportion of ptarmigans as prey at 25.0%.

Compared to previous video monitoring studies in Norway, I found a distinctly higher gross prey mass. This is the case for both studies with one nestling and for other studies with two nestlings like mine. I found a total gross mass of 140 273 g which is 51 013 g more than (Skouen, 2012), who recorded the gross mass that was closest to my results. This may be a result of the number of mountain hares delivered in my study. I recorded 33 hares delivered with an estimated total gross mass of 66 500g, which is a marked increase in hares as prey compared to previous video monitoring studies, that found the number of hare deliveries to be between 13 to 20 per nest (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021). This disparity in the number of hares delivered could explain in part why I found a much larger gross mass than previously recorded. The gross mass of hares alone accounted for 47.4% of the total gross mass from all delivered prey. The total gross mass of hares from my study was around twice as much as previous video monitoring studies where the gross mass of hares was between 22 000 g to 33 000 g. While my total gross mass was much higher, the mean gross mass of 495 g found in my study is within the interval of gross mass found in previous video monitoring studies (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021).

Small rodents were not an important prey group in either numbers or gross mass, with 19 voles (Microtus spp.) and no Norway lemmings recorded in my study. Voles made up 6,7% of the delivered prey and only 0,7% of the gross prey mass. When performing line transects to estimate game bird populations Hønsefuglportalen additionally registers small rodent observations. The purpose is not to estimate rodent population density, therefore the results should be considered carefully. However, these estimates may indicate the density of the small rodent population in the study area and in turn the availability of small rodents as a prey group. In 2022 small rodents were only observed in 5% of taxation efforts in Oppland County (Now Innlandet County). The small rodent population in the area had its last peak in 2018 when small rodent observations occurred for nearly 75% of taxation efforts. This correlates well with the results of Günther (Günther, 2020) who recorded a large proportion of lemmings and voles in 2018 during the peak, and no lemmings and few voles in 2019 after the population crashed (Günther, 2020; Hønsefuglportalen, 2023). The absence of lemmings as prey in my study, and only one lemming recorded by (Mjelde, 2021) can probably be partially explained by their low population densities in the area for the period 2019 to 2022.

The large variation of prey species and variations in mammalian and avian prey proportions in the diet of the golden eagle highlights the species' flexibility as a generalist predator. Nearly half of the avian prey in my study were thrushes, while few voles were delivered, and lemmings were completely absent. This corresponds to the findings of Mjelde (Mjelde, 2021), but differs from previous video monitoring studies in Norway (Skouen, 2012; Dihle, 2015; Günther, 2020), which found a higher number of small rodents. Mjelde (Mjelde, 2021) suggests that in years of low small rodent densities, thrushes could be an alternative prey to small rodents, and thereby explain the high proportion of thrushes as prey found in her study.

Domestic sheep as prey

During my study, remains of domestic sheep were delivered at the nest on five separate occasions. Depredation on domestic livestock is the cause of debate in Norway, especially related to domestic sheep and domestic reindeer. In each case the sheep remains delivered it was only one leg or both legs connected at the hip. When comparing the size of the leg to the size of the eagle, they likely originated from both adult sheep and lambs. Previous studies from Fennoscandia have found that golden eagles have delivered remnants of both sheep and reindeer at the nest during the breeding season. This has been found in both more traditional studies using prey remains and pellets collected at the nest (Tjernberg, 1981; Warren et al., 2001; Nystrom et al., 2006; Johnsen et al., 2007) and in one video monitoring study in Norway (Günther, 2020).

Compensation for livestock lost to predation is paid to farmers from the Norwegian government, to recoup lost income. Still, livestock predation by predators whose population has increased in the last decade is a controversial topic. Rovbase registers all reports of livestock harmed or killed by the largest Norwegian predators. Additionally, Rovbase makes an overview of how many farmers receive compensation for livestock harmed or killed by a predator, and what predator is responsible, sorted by county or municipality. As several Norwegian counties were merged into larger ones, I will be using data for 2022 from the three municipalities closest to my study area. In Gausdal, Sør-Fron and Nord-Fron municipalities a total of 494 sheep were compensated for due to damage by predators, 149, 100, and 245 sheep, respectively. The golden eagle was registered as the predator for 12 lambs in Gausdal (8.1%), 2 lambs in Sør-Fron (2.0%), and 14 lambs in Nord-Fron (5.7%). In total 28 lambs, across three municipalities, were registered as damaged or killed by the golden eagle, making up 5.6% (N=494) of all compensated sheep livestock in the area. The main livestock predators of this area were the Eurasian lynx (*Lynx lynx*) and the wolverine (*Gulo gulo*), responsible for 61.5% and 32.7% of compensated livestock damages in the area respectively (Rovbase, 2022a).

As the golden eagle is known to feed on carrion (Newton, 1979; Watson et al., 1992; Watson, 2010; Katzner, 2020), it is possible that the sheep remains delivered at the nest during my study were remains from already dead individuals. The eagles could have found the sheep dead from illness or injury, or as remains from a kill originally perpetrated by a lynx or a wolverine. On the basis of the video clips and the condition of the sheep remains, it is not possible to accurately determine if the delivered sheep remains in my study were killed by the golden eagle.

Proportion of prey

Thrushes were the most numerous prey type of all prey delivered to the nest. The probability of prey being a thrush increased with nestling age. Previous video monitoring studies have also found a positive relationship between the probability of a prey being a thrush and the nestling age (Dihle, 2015). When the nestlings were approximately 85 days old there was a 50% probability of any prey item delivered being a thrush. Thrushes were the most numerous prey species accounting for 33.2% of all prey items delivered. The number of thrushes changed markedly throughout the study period, in the two first periods of the nestling ages from 6 to 62 days old, thrushes represented 20% and 22% of all prey deliveries respectively. But when nestlings entered the last age stage from 63-91 days old thrushes represented 45% of all delivered prey items. This distinct increase in thrushes as prey might be explained by the availability of thrushes, especially nestlings and fledglings, within the golden eagle's territory later in the breeding season. In previous studies Dihle (2015), Nygård (2015) and Mjelde (2021) also mentioned the availability of thrushes being higher later in the season, as thrush fledglings are more available then. Additionally, thrushes are smaller prey items that may allow the nestlings to handle them unassisted (Slagsvold & Sonerud, 2007; Sonerud et al., 2014b), making them a more attractive prey when nestlings are older and capable of handling prey unassisted.

The probability of prey being a ptarmigan decreased with nestling age. As the nestlings grew older the probability of any delivered prey item being a ptarmigan decreased. Ptarmigans were the second most numerous prey species with 14.8% of all delivered prey items. Like thrushes, the proportion of ptarmigans in the diet changed throughout the study period. Ptarmigans were the most numerous prey in both the first and the second age groups, from 6 to 33 days and from 34 to 62 days, accounting for 25.8% and 25.0% of delivered prey respectively. While in the last age group from 63 to 91 days ptarmigans were the fourth most numerous prey accounting for only 5.5% of all delivered prey. My results correspond with previous studies that also found that the probability of a delivered prey being a ptarmigan decreased with nestling age (Skouen, 2012; Dihle, 2015; Nygård, 2015; Mjelde, 2021). Ptarmigans may be more available prey early in the breeding season and have chicks earlier than other birds like the thrush, making them more attractive prey early in the breeding season. The nestlings in my study started to feed unassisted later than previously recorded, and the most dramatic change in prey composition was before and after the nestlings were 63 days old, which is slightly after they started to feed unassisted consistently. Ptarmigans are a larger prey with a mean mass of 481 g, compared to the thrush with a mean mass of 93 g in my study. Which may further explain why fewer ptarmigans were delivered as the nestlings grew older, as the golden eagle parents delivered smaller prey items with nestling age to allow the nestlings to handle prey unassisted.

The probability of prey being a hare was not affected by nestling age, but tended to decrease as the nestlings grew older. Hares were the third most numerous prey species with 11.6% of all delivered prey. The proportion of hares in the diet remained quite similar for all three age groups with a slight decrease which was not significant. Hares were the third most numerous prey for the first two age groups with 15.5% and 12.5% respectively. In the third age group hares were the second most numerous prey with 9.7% of all delivered prey. Hares accounted for the largest proportion of prey mass both throughout the entire study and for each age group. Hares were typically some of the largest prey items delivered at the nest, and the nestlings were not recorded handling a mountain hare completely unassisted in my study.

Early in the nesting season the male is mainly responsible for hunting while the female shields the nestlings and assist with partitioning and feeding prey items. As long as the female is handling the prey, the size of the prey items is not as important, as it is not limited by the nestlings' gape size or handling capabilities. Prey such as ptarmigans and hares may not be selected when the nestlings are older as they are mostly too large for the nestlings to handle unassisted (Mjelde, 2021). Making them a more attractive prey earlier in the nestling season when the female handles prey regardless of size. While smaller prey such as thrushes are more important when the nestlings are older since they can be handled unassisted, allowing the female to leave the nest more often and join the hunting effort (Slagsvold & Sonerud, 2007).

Diel delivery pattern

The golden eagles were active for most of the day and prey delivery was recorded in 22 out of the 24 hour-blocks in one day. A prey delivery was more likely than random to occur between 07 hours and 18 hours, the earliest prey delivery being recorded at 03:41 and the latest being recorded at 00:13. My data of the diel delivery pattern showed that the golden eagle is a diurnal bird, which corresponds to the literature (Watson, 2010) and previous video monitoring studies (Günther, 2020; Mjelde, 2021). The diel delivery pattern presented itself as two peaks throughout the day, where the first peak in the morning had the highest probability of delivery and the second peak in the evening had a lower probability of delivery. The diel delivery pattern found in my study with two peaks was similar to the pattern found by Günther (2020), while Mjelde (2021) found a diel delivery pattern with only one peak.

The difference in the diel delivery pattern may be explained by the difference in the proportion of prey species. Mjelde (2021) found a larger proportion of avian prey in the diet than both I and Günther (2020) did, and Mjelde (2021) partly attributes the lack of a second peak in the delivery pattern to the low numbers of mammalian prey in her study. My results may be explained by the presence of both mammalian and avian prey, as many of the mammalian prey species in my study are nocturnal, while most of the avian prey in my study are diurnal. This diel delivery pattern is further reinforced when exploring the overlap of delivery density between some of the main prey species.

When only mammalian prey was considered, prey were delivered with quite similar probability throughout the day, however, there was one peak around 08 hours, with a tendency to a second peak around 16 hours, but this peak was small and not significantly higher than what could be randomly expected. Mammalian prey were delivered with a higher probability than randomly expected from 07 hours until 13 hours. The diel delivery pattern for mammals found in my study was similar to that found by both Günther (2020) and Mjelde (2021) , with only a shorter time of day having a probability of delivery higher than random.

The diel delivery pattern of avian prey was divided into three peaks that were not very different from one another, and the probability of avian delivery was higher than randomly expected from 07 hours until 18 hours. In the diel delivery pattern of avian prey, the peaks showed a lower probability of delivery with the initial peak around 08 hours and the second peak around midday showing a similar probability of a prey delivery. The third peak was lower and did not show a probability of prey delivery significantly higher than randomly expected. Avian prey was delivered to the nest with similar diel delivery patterns to those found in previous studies (Günther, 2020; Mjelde, 2021). Avian prey delivery occurred throughout most of the day and had a probability higher than random from 8 to 9 of the 24 hours of the day (Günther, 2020; Mjelde, 2021).

Activity pattern and overlap.

Mammalian prey had a peak in frequency of delivery from around 09 hours until 11 hours, which is earlier in the day compared to avian prey which had a peak from around 12 hours util 14 hours. The activity pattern of prey delivery for mammalian prey and avian prey was similar to the diel delivery pattern that I found for the same prey groups. When comparing the density of delivery for each hour block for mammals and birds I found some overlap in the delivery pattern. Although, with separate peaks where mammals were more likely to be delivered earlier in the day while birds had their delivery peak around midday.

The pattern found when comparing mammals and birds was also found when comparing some of the most important prey species, the mountain hare, and the thrush. A similar pattern was found again when comparing voles to thrushes. Both mountain hares and voles are nocturnal species whose activity may overlap with the golden eagle early in the morning and in the evening (Kildahl, 2020; Pettigrew et al., 2021), which may explain the delivery density pattern found in my study. Thrushes, like the golden eagle, are diurnal birds (Watson, 2010; Byrkjedal et al., 2012), and therefore available as prey for most of the eagles' active hours and had the highest delivery density around midday.

Density pattern and overlap analysis are originally meant for camera trap data registering passing individuals, then comparing species' density for each hour of the day in that location (Ridout & Linkie, 2009). In my study, I do not register living individuals and compare them to their predator, the golden eagle, but rather registering the temporal distribution and density of prey species delivered at the nest. The activity of each prey species is not recorded directly, rather at what times during the day each prey is caught by the eagles is recorded. This should give a picture of the temporal availability of each species or group of prey since their availability as prey is likely related to when and at what density they occur in the eagle's diet.

Effect of nestling age

Number of prey delivered at the nest per day increased with nestling age until the time for fledgling was close and fewer prey were delivered. Previous studies of single-prey loaders such as the Eurasian kestrel (*Falco tinnunculus)* and the great tit (*Parus major)* have found a positive relationship between delivery rate and nestling age (Barba et al., 2009; Steen et al., 2012). The delivery rate found in my study corresponds to that of previous studies, including video monitoring studies of golden eagles in Norway (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021). Although the delivery rate increased with nestling age, I did not find a significant relationship between nestling age and net prey mass delivered per day. This result does not correspond with a previous study that found the net prey mass delivered per day for the Eurasian kestrel to be positively related to nestling age (Steen et al., 2012). My results do not support the expected increase in net prey mass delivered as a result of increased food demand.

Number of prey items delivered at the nest per day increased with nestling age, which is supported in the literature (Barba et al., 2009; Steen et al., 2012). At the time when nestlings are able to handle most or all prey items unassisted, the female is free to join the male in hunting and delivering prey without being as tied to the nest or immediate surrounding areas (Slagsvold & Sonerud, 2007; Watson, 2010). At this age the nestlings are able to thermoregulate themselves and are no longer so dependent on the female to shade them from the sun or shield them from rain or wind, which further allows the female to leave the nest (Newton, 1979; Watson, 2010). The increase in prey deliveries per day corresponds well with the days when the nestlings started to consistently handle prey unassisted. Similarly, to Mjelde (2021), I found that the number of prey deliveries decreased as the nestlings came close to fledging. This behavior may be an attempt to motivate the nestlings to fledge, and the parents were observed to fly past the nest several times with prey without landing on the nest and delivering it to the nestlings (personal observation). The fact that there was an increase in the delivery rate but no corresponding increase in delivered net prey mass may be explained by the increase in the delivery of smaller prey items. There is an expected increase in food demand (Collopy, 1986) which was not found in my study. There can be multiple explanations for this result, one being that neither parent self-fed from prey items delivered to the nest after the nestlings started to feed unassisted. Early in the nesting season the female often fed on delivered prey from the male as she rarely could leave the nest to feed herself. Later, when nestlings handle prey unassisted the parents spend little time on the nest, only to partition the larges prey items, and most delivered prey is only fed on by one or both nestlings. Therefore, the nestlings eat a larger portion of the prey mass delivered, even though the delivered mass did not significantly increase the amount ingested by the nestlings may still have increased with age. Further, larger prey items have a larger proportion of mass that is not ingested, as the unusable parts of the animal are also larger (Slagsvold & Sonerud, 2007; Slagsvold et al., 2010). Proportionally to the size of the prey, there are more leftovers from larger prey items (Slagsvold et al., 2010), which might contribute to the delivered net mass not increasing with nestling age, and the increase in the number of prey deliveries. Additionally, in my study two nestlings fledged, and the net mass delivered was higher than observed in previous video monitoring studies. This indicates that the nestlings received a sufficient amount of prey items.

The male delivered 87 % of prey items for the deliveries where the sex of the delivering parent was determined. This is a higher percentage than in previous video monitoring studies which have found the male to deliver between 57% and 70% (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021) The male spends most of his time during the breeding season hunting and delivering prey at the nest, provisioning for both the female and the nestlings. The female spends most of her time on the nest incubating eggs, brooding and shielding nestlings, and partitioning prey items for the nestlings (Watson, 2010). As the nestlings grew older, they can handle some of the prey unassisted and need more food, therefore the female joins the male in hunting and delivering prey later in the breeding season (Sonerud et al., 2014b). The female contributed with few prey deliveries, however, she was more likely to deliver heavier prey than the male, who instead delivered a large quantity of smaller prey items. The interaction between the sex of the delivering parent and nestling age had a significant effect on gross prey mass. The male delivered smaller prey with lower gross mass as the nestlings grew older, while the female tended to deliver larger prey as the nestlings grew older.

A potential cause of the exceedingly strict parental roles found in my study may be the high mean net mass per prey recorded. Larger prey items require more handling and the prey mass had negative relationship with the probability of a nestling handling a prey item unassisted. The nestlings were assisted almost exclusively by the female and the nestlings started to feed unassisted later than what recorded in previous studies. With a high mean prey mass per prey item the female might have needed to assist the nestlings more than in previous studies leaving her less time to hunt off the nest. This in turn led to the increased division in parenting roles in terms of prey delivery as recorded in my data.

As the nestlings grew older the male delivered prey items with a lower gross mass, and the male was likely to deliver smaller prey items than the female. Gross mass delivered by the female did not have a significant relationship with nestling age. Steen (Steen et al., 2010; Steen et al., 2012) found that in the Eurasian kestrel the average prey body mass decreased with nestling age, and males have been found to deliver smaller prey items than the female (Sonerud et al., 2013). Similarly, Mjelde (2021) found a decrease in average gross mass with nestling age, with the male delivering smaller prey than the female.

The observed decrease in gross prey mass in relation to nestling age may allow the nestlings to start handling unassisted earlier, thereby enabling the female to resume hunting (Sonerud et al., 2014b). Earlier in the nestling season the probability of a larger prey was higher, as the female assisted the nestlings with all delivered prey items. When the nestlings were able to handle prey unassisted the gross prey mass decreased. Allowing the nestlings to handle a larger portion of delivered items unassisted, freeing the female to resume hunting.

Prey handling prior to delivery

The probability of a prey item being delivered decapitated decreased with nestling age and was not affected by the gross body mass of the delivered prey item. As the nestlings grew older fewer prey were delivered decapitated. This may be due to the increased gape size of the nestlings as they grew, allowing them to swallow the head of larger prey without difficulty or danger. The nestlings´ ability to handle prey with increased skill and strength as they became older and more experienced may also be a reason. Smaller prey items tended to be less likely to be decapitated than larger prey items, which may again be due to the development of the nestlings´ gape size. For prey items with a higher body mass, the head would be too large for nestlings to swallow, especially for avian prey where the beak might be an additional obstacle. When the head cannot be swallowed whole the value of it as a food item may decrease as it is difficult to open and partition due to the hard skull (Slagsvold & Sonerud, 2007). This may be a reason why the parents decapitate larger prey prior to delivery. The head of larger prey can be heavy and therefore not profitable to carry to the nest if it cannot be consumed. A prey was most likely to be delivered decapitated when the nestlings were young and the gross prey mass was large, consequently, a prey was most likely to be delivered with the head present when the nestlings were older, and the gross prey mass was small. One reason as to why there was no significant relationship between the probability of decapitation and the gross prey mass might be related to the avian prey in the diet. Avian prey had a mean gross mass of 299.2 g while mammalian prey had a mean gross mass of 1192,2 g. Thus, there was a larger portion of smaller prey that were birds. The risk associated with swallowing the head of a bird with a protruding beak is larger than swallowing a narrower mammalian prey item. In a study of Eurasian kestrels Steen (Steen et al., 2010) found that the probability of decapitation decreased with nestling age, but that avian prey were decapitated for a longer part of the nestling period than mammalian ones, due to the risk of consuming the head of a bird. Since many of my smaller prey items were birds, they were likely decapitated for a longer part of the nestling period than what would be expected for that prey mass, to avoid the risk of a nestling choking or injuring itself. This might explain why there was no significant difference in the probability of prey being decapitated in relation to gross prey mass.

I did not find any significant effect of any of the tested variables on the probability that avian prey was plucked prior to delivery, where the model containing gross prey mass was chosen as the best fitting model. As only avian prey could be plucked, I excluded all mammalian prey from the models and statistical analysis, so they would not conceal any potential relationships. Regardless there was not a positive effect of gross prey mass on the probability of an avian prey being delivered plucked.

During the nesting season golden eagles are limited by their nest location and need to return to the nest regularly with prey (Stephens et al., 2007; Davies et al., 2012). Capturing larger prey gives more energy per prey item allowing the eagles to capture and deliver a smaller number of prey (Barbosa & Castellanos, 2005; Davies et al., 2012). However, larger prey are more demanding both to capture and to carry back to the nest, where the nestlings will need assistance in handling. The handling time is longer for larger prey and the female must open the skin and help partitioning even when nestlings are older. This constrains the female to the nest allowing her less time off the nest to hunt for new prey (Sonerud et al., 2014b). In relation to prey mass, less of the proportion of the prey is consumed for larger prey than for smaller, where typically most of the prey item is consumed (Slagsvold et al., 2010). In combination with the nestlings' ability to handle smaller prey unassisted, it may be more profitable for the golden eagle parents to deliver a larger number of small and medium-sized prey items rather than a few large ones.

Nestling unassisted handling

In my study the first instance of a nestling handling unassisted was when it was 32 days old. The age at which nestlings start handling prey unassisted is subject to variation, with earlier video studies recording nestlings being 28 (Dihle, 2015), 55 (Nygård, 2015), 44 (Günther, 2020), and 27 days old (Mjelde, 2021). However, it is worth mentioning that the first unassisted handling in my study was one of the golden eagle nestlings swallowing whole two thrush nestlings without partitioning, plucking, or any further handling. The first time a nestling handled a prey unassisted by dismembering it was a vole at 56 days old.

I found that the nestlings handled prey unassisted in 39.6% of the recorded prey deliveries. This is lower than the percentage found in previous video monitoring studies from Norway that found the nestlings to have handled between 43% and 79% of the delivered prey items unassisted (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021). The proportion of delivered prey that was handled unassisted reached 50% when the nestlings were 58 days old for small prey items, and 78 days old for the mean mass of prey items, which is 10 to 20 days later than what was found in previous studies. Dihle (2015) found the 50% limit to be at 47 days, Nygård (2015) at 49 days, while other studies found the 50% limit to be as early as 40 days old (Sonerud et al., 2014a; Mjelde, 2021). Further, I found that the probability of unassisted handling increased with the age of the nestlings and decreased with net prey mass. The highest probability of unassisted feeding was found when the nestling age was high, and the net mass of the prey was low. This result is supported by previous studies (Skouen, 2012; Sonerud et al., 2014b; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021).

The first observation of unassisted handling was quite early in my study; however, the nestlings did not consistently start handling unassisted until they were 58 days old, which in turn is quite late. This did not allow for a lot of time when the nestlings were handling unassisted which could explain the low percentage of unassisted handling recorded in my study. Additionally, the mean prey mass was higher than what was found in earlier studies (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020; Mjelde, 2021) which may have prevented the nestlings from handling unassisted earlier and handling a larger proportion of the delivered prey items. Larger prey items are more difficult to handle and often require the parent to open the skin or plucking fur or feathers before the nestlings can ingest the prey (Sonerud et al., 2014b). I also recorded few small mammals which are easier for a young nestling to eat than small birds, as they often can be swallowed whole (Steen et al., 2010). As the nestlings grew, they became able to handle more and larger prey unassisted as both their strength and gape size developed (Slagsvold & Sonerud, 2007). The smaller prey were handled unassisted earlier than the larger ones, and for the larger prey like hares, the female would occasionally assist in partitioning until the day the last nestling fledged.

For further studies

During my study I only observed one golden eagle pair at one nest location. While my data may give insight into the diet and prey handling of golden eagles during the breeding season in my study area, my data on the golden eagle diet might not be representative of other locations or even the same location outside the breeding season. The golden eagle is known as a generalist raptor capable of local and seasonal adaptations in prey choice (Watson, 2010). Their distribution ranges from most of the Palearctic to northern Africa, encompassing a wide range of landscapes and potential prey species (Katzner, 2020). Therefore, my data should be considered with care regarding locations outside the Fennoscandian mountainous areas.

To further strengthen the results presented in my thesis and the previous video monitoring studies, one should investigate several nests with a greater geographical dispersal, over multiple years. A larger dataset spanning over a longer time series could reveal potential local differences, differences between years, and the differences in success between golden eagle pairs. A longer time series would also allow further study of the effects of the weather, both directly on nestling survival, but also indirectly on the distribution and availability of prey species (Steenhof et al., 1997).

Additionally, video monitoring studies do not take into consideration the diet outside the nesting season. Golden eagles have a varied diet throughout the year, and younger, unestablished, individuals appear to have a different diet than breeding pairs, and are more likely to predate on livestock (Watson, 2010). GPS surveillance can mitigate some of the uncertainties of video monitoring at the nest. Advancements in technology allow researchers to visit cluster sites where the eagle has spent time hunting or eating. When approaching the kill site directly it is easier to decide whether the eagle killed the prey themselves or is simply feeding on a carcass. This method is time consuming and often expensive but allows clearer insight to diet outside the breeding season and the diet of unestablished younger individuals (Mattison, 2022). However, like nest inspections and pellet analysis, this method can overestimate the presence of larger animals in the diet. The eagles leave more remains of larger animals and spend longer time handling them (Slagsvold et al., 2010; Sonerud et al., 2014b). While a smaller prey like a vole or a tit may be swallowed whole in only a few seconds, leaving little to no remains. Additionally, a study done in northern Norway mounted mortality-sensing radio-collars on semi-domestic reindeer calves and females to determine how many animals were predated on by the golden eagle (Nybakk et al., 1999). The different methods all present different challenges, to deliver the most accurate representation of the golden eagle’s diet and prey choice, a combination of several methods might be applied over a longer study period.

In terms of management implications, one should focus on areas where the reported domestic livestock predation of golden eagles is high. Such studies could help determine how prevalent domestic or semi-domestic livestock is in the breeding diet of the golden eagle. However, determining if the golden eagle is the predator or simply found the prey as carrion is very difficult to determine with video monitoring. A study combining GPS data with radio tracking and video monitoring at the nest could help mitigate the uncertainties of exclusively video monitoring. Each method has weaknesses on its own, but when combined one could get fairly accurate knowledge of the occurrence and extent of domestic livestock predation perpetrated by the golden eagle. However, while my method of video monitoring is quite cost-effective and causes little disturbance for the breeding eagle, radio-tracking is both expensive and a license to track birds of prey by GPS-tags has been difficult to obtain in Norway as of late due to concerns about the animal’s well-being. Monitoring methods should be evaluated by how cost effective they are and how invasive they are to the species being studied.

Conclusion

In my study, I found that birds were the most numerous prey group during the breeding season of the golden eagle. Thrushes were the most numerous prey followed by ptarmigans and mountain hares. Thrushes were more important than expected, highlighting that thrushes may be an important alternative prey species for years when ptarmigan and rodent abundance is low. In terms of biomass mammals were the most important group, with mountain hares accounting for the largest proportion of delivered prey mass, followed by ptarmigans. The remains of domestic sheep were delivered as prey items on five separate occasions. By only looking at the videos it was not possible to determine if the eagles killed the sheep or found them as carrion before delivering them at the nest. As the nestlings grew older the parents altered the selection of prey size from larger prey earlier to delivering smaller prey later in the breeding season. Delivering smaller prey would allow the nestlings to start handling unassisted earlier and handle a larger proportion of delivered prey items without assistance from either parent. Further studies using video monitoring should be conducted over long time series and at multiple locations, to best investigate the overall breeding diet, local variations, and potential yearly trends. Combining video monitoring and tracking of the adult birds could help determine the prevalence of predation on domestic or semi-domestic livestock, versus livestock as carrion in the diet.

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Appendix A

The model selection from AIC, finding the logistic regression model that most accurately predicts the diel delivery pattern of the golden eagles in my study.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
1	PreyDelivery~I(cos(2*pi*Hour/24))+ I(sin(2*pi*Hour/24))	3	121.05	0.00	0.70
2	PreyDelivery~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))	4	123.05	1.99	0.26
4	PreyDelivery~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))+ I(cos(4*2*pi*Hour/24))+I(sin(4*2*pi*Hour/24))	3	127.55	6.50	0.03
3	PreyDelivery~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))	4	129.50	8.45	0.01
5	PreyDelivery~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))+ I(cos(4*2*pi*Hour/24))+I(sin(4*2*pi*Hour/24))+ I(cos(5*2*pi*Hour/24))+I(sin(5*2*pi*Hour/24)	2	234.46	113.40	0.00
0	PreyDelivery~1	2	253.50	132.45	0.00

Appendix B

The model selection from AIC, finding the logistic regression model that most accurately predicts the diel delivery pattern of mammalian prey for the golden eagles in my study.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
2	PreyDelivery~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))	4	123.05	1.99	0.26
1	PreyDelivery~I(cos(2*pi*Hour/24))+ I(sin(2*pi*Hour/24))	3	121.05	0.00	0.70
3	PreyDelivery~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))	4	129.50	8.45	0.01
5	PreyDelivery~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))+ I(cos(4*2*pi*Hour/24))+I(sin(4*2*pi*Hour/24))+ I(cos(5*2*pi*Hour/24))+I(sin(5*2*pi*Hour/24)	2	234.46	113.40	0.00
0	PreyDelivery~1	2	253.50	132.45	0.00

Appendix C

The model selection form AIC, finding the logistic regression model that most accurately predicts the probability of an avian prey being plucked prior to delivery at the golden eagle nest.

Model	Explanatory variable	K	AICc	Δ AICc	AIC weight
7	Gross body mass	2	177.05	0.00	0.62
6	Nestling age + Gross body mass	3	178.80	1.75	0.26
5	Nestling age * Gross body mass	4	180.52	3.47	0.11
3	Delivering sex	2	186.02	8.97	0.01
2	Nestling age + Delivering sex	3	187.74	10.70	0.00
1	Nestling age * Delivering sex	4	189.83	12.78	0.00
0	Intercept	1	193.58	16.53	0.00
4	Nestling age	2	195.03	17.98	0.00

Appendix D

Generalized linear models for investigating the effect of nestling age on the selected response variables.

Response variable	Explanatory variable	Distribution
Probability of thrush	Nestling age	Binomial
Probability of ptarmigan	Nestling age	Binomial
Probability of hare	Nestling age	Binomial
Number of prey deliveries per day	Nestling age	Poisson
Net prey mass delivered per day	Nestling age	Normal

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