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The golden eagle's (*Aquila chrysaetos*) diet and prey handling at the nest investigated by video monitoring

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Acknowledgements

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Abstract

A parent bird provisioning for its nestlings faces many decisions, which are important for the nestlings' survival. As the nestlings grow older, their needs and demands may change, and the parent may respond to this by altering prey selection and handling of prey before delivery at the nest. I investigated the diet and components of the breeding behaviour of the golden eagle (*Aquila chrysaetos*) at the nest. Previously, the breeding diet has mainly been researched by collecting prey remains and pellets, which is largely biased. By video monitoring, the breeding diet will be estimated more accurately, and one can investigate more variables and behaviours at the nest. In this study, one golden eagle's nest in Norway was video monitored during the breeding season, from the 19th of May to the 29th of August in 2020. The breeding diet of the golden eagles consisted of 88.5 % avian prey. Mountain hares (*Lepus timidus*), thrushes (*Turdus* spp.), and ptarmigans (*Lagopus* spp.) were the most abundant prey in quantity and gross mass. The probability of decapitation decreased with nestling age, plucking increased with gross bird mass, and the probability of a prey being partly eaten decreased with nestling age and increased with gross prey mass. The delivery pattern of the golden eagles had one peak during the day and a probability of delivery higher than random between 09:00 and 16:00. The number of delivered prey items per day increased with nestling age, while the net delivered prey mass did not. As the female resumes hunting, the number of prey delivered will increase, but a decreasing prey mass likely cancelled the corresponding increase in delivered prey mass. The gross prey mass decreased with nestling age, and the male delivered smaller prey than the female. Also, the male had a less decreasing probability of delivering smaller prey than the female as the nestlings grew older. The probability of a delivered prey being a thrush increased with nestling age, and the male was more probable of delivering a thrush than the female. As the nestlings grew older, the female had a larger increase in the probability of delivering a thrush than the male. The probability of the nestlings handling prey unassisted increased with nestling age and decreased with net prey mass. When the nestlings were handling unassisted, the handling time increased with net prey mass. The gross handling time increased if none of the nestlings monopolised the prey. The probability of the nestlings swallowing a prey whole decreased with nestling age and net prey mass, and the probability of them plucking a bird increased with nestling age. During the nestling period, the largest nestling handled more prey mass than the smaller nestling. My study support that the golden eagle has a broad diet, which also changes through the breeding season to enable the nestlings to handle prey unassisted.

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Introduction

A predator affects its ecosystem by restricting the distribution and abundance of its prey and thereby influencing the community organisation (Krebs, 2014). For a hunting predator, the optimal prey choice will depend on the energy content of the prey, the handling time and the search time (Davies et al., 2012). At times when a predatory bird forages for dependent young, the optimal prey choice may be more complicated. A parent bird needs to collect and deliver food to its nestlings to ensure survival and fuel their growth (Ydenberg, 2007). During the breeding season, the prey availability and selection when provisioning will affect the parent bird's reproductive success (Newton, 1979; Moss et al., 2012). The selection of prey when provisioning will depend on the prey's energy content, the distribution of prey, the prey density, and the travel time (Ydenberg, 2007). For each potential prey the parent bird detects, it must decide whether to ignore, capture and eat the prey or catch and deliver it to the nestlings (Davoren & Burger, 1999; Ydenberg, 2007). After capturing a prey, the parent may also choose to prepare the prey item before delivering it to the nest (Sodhi, 1992; Rands et al., 2000). As the nestlings develop, their growth rate is not constant (Collopy, 1986; Barba et al., 2009). Therefore, the nestlings' demands and needs may change through the nestling period, and the parents may need to respond to these changes when selecting prey.

The diet of raptors during the breeding season has been extensively researched (Tjernberg, 1981; Steenhof & Kochert, 1988; Grønnesby & Nygård, 2000; Selås et al., 2007). Earlier, raptor diet could be examined by stomach contents (Watson, 2010) or by direct observations from blinds or long distances (Collopy, 1983), but these methods are either highly invasive or time-consuming. Another method has been to collect prey remains and pellets, which has been primarily used when estimating the raptor breeding diet (Tjernberg, 1981; Marquiss et al., 1985; Steenhof & Kochert, 1988; Simmons et al., 1991; Högström & Wiss, 1992; Redpath et al., 2001; Rutz, 2003; Nyström et al., 2006; Strann et al., 2013). Collecting pellets and prey remains are time-consuming and can result in biased results since the delivered biomass and the total number of prey items are underestimated (Collopy, 1983; Sulkava et al., 1998; Lewis et al., 2004; Harrison et al., 2019). Additionally, uncommon species are poorly registered (Lewis et al., 2004), and prey groups and sizes are either under- or overestimated (Simmons et al., 1991; Sulkava et al., 1998; Redpath et al., 2001; Selås et al., 2007; Harrison et al., 2019). By combining the results of pellets and remains, the accuracy increases (Simmons et al., 1991). The proportions of the primary prey taxon will also be close to the registered proportions from direct observations (Collopy, 1983). Still, estimating raptor diet by collecting pellets and remains are not ideal, as it is largely biased.

In later years, technological advances have introduced new possibilities for estimating raptor diet. Now, it is possible to video monitor raptor nests during the breeding season (Steen, 2009). This method not only reduces biases, as one can watch clips several times and get second opinions, but also enhances the opportunity for looking at several behaviours and variables from one monitoring. Additionally, more individuals and prey categories can be registered, and a better estimate of delivered biomass and age structure of the raptor's prey delivered at the nest can be obtained (Lewis et al., 2004). Some studies have combined the collection of pellets and prey remains, and video monitoring the nests (Lewis et al., 2004; Selås et al., 2007; Tornberg & Reif, 2007). In one of these, six prey species were only found when video monitoring the nest (Lewis et al., 2004). Others have only used video monitoring (Grønnesby & Nygård, 2000; Steen, 2010), and Sonerud et al. (2014a) monitored 61 nests distributed on 9 raptor species. Even though there is still some uncertainty when identifying prey (Harrison et al., 2019), video monitoring is the most accurate method for estimating the breeding diet of raptors (Lewis et al., 2004).

The diet of raptors, i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes), can vary considerably as they have a specialised bill, making them able to partition prey and thus relieving them from swallowing constraints (Slagsvold & Sonerud, 2007). When partitioning prey, the time needed to handle prey thus increases considerably (Slagsvold & Sonerud, 2007). Partitioning prey also enables raptors to consume large prey relative to their body mass, and therefore, exploit many prey species (Kaspari, 1990). For instance, the golden eagle (*Aquila chrysaetos*) has been registered to prey upon 76 different prey species (Sulkava et al., 1998). In most raptors, the female is larger than the male, and during breeding, the male hunts and provides the food while taking no part in brooding and feeding the nestlings (Newton, 1979; Watson, 2010). The larger female incubates, broods and feeds the nestlings, and may hunt later in the nestling period (Newton, 1979; Watson, 2010).

The golden eagle is one of the world's largest predatory birds and a generalist inhabiting many open habitats (Watson, 2010; Katzner et al., 2020). It has a wide geographical range, and resides throughout the Palearctic, into northern Africa, and can also be found in many places in North America (Watson, 2010; Katzner et al., 2020). With a mass that can reach 5 kg and a wingspan of more than 2 m (Watson, 2010), the golden eagle is Norway's second largest raptor, only the white-tailed eagle (*Haliaeetus albicilla*) is larger (Halley, 1998; Halley & Gjershaug, 2008). In Norway, the golden eagle breeds in 10 out of 11 counties, and the estimated number of occupied territories is 936 (Dahl et al., 2015). As apex predators, like the golden eagle, shape their inhabited ecosystems, knowledge about the golden eagle's ecology and diet are essential to understand ecological dynamics (cf. Estes et al., 2011).

The golden eagle is a generalist, with a considerable variation in both prey species and sizes. The large raptor captures prey ranging from 10 g to 5800 g (Steenhof & Kochert, 1988), and predation on lambs of domestic sheep (*Ovis aries*) and red deer (*Cervus elaphus*) calves of 30 kg has also been reported (Bergo, 1990). Still, the golden eagle mainly hunts medium-sized birds and mammals (Katzner et al., 2020), and the most common prey in the North-west Palearctic are game birds (Galliformes) and lagomorphs (Lagomorpha) (Cramp, 1980; Sulkava et al., 1998; Watson, 2010). In Norway, the golden eagle may also predate domestic sheep (Warren et al., 2001) and reindeer (*Rangifer tarandus*) (Johnsen et al., 2007). Johnsen et al. (2007) reported a total of 8.5 % reindeer in the golden eagle's diet, and Stien et al. (2016) reported the golden eagle to kill 23 % of all lost lambs in certain areas. In 2020, the Norwegian government compensated farmers for 1 307 sheep (Miljødirektoratet, 2020a) and reindeer herders for 6 568 reindeer, presumably killed by the golden eagle (Miljødirektoratet, 2020b). Therefore, knowledge about the extensiveness of killing lambs and reindeer is important as the golden eagle's diet may also have implications from a socio-economic perspective.

The golden eagles' diet and behaviour during the breeding season are influenced by their prey populations, and their breeding success is affected by available prey in the area surrounding the nest (Moss et al., 2012). When the golden eagles are provisioning for their nestlings, they not only hunt and collect food but may also prepare the prey before and after delivery at the nest before feeding it to the nestlings (Sonerud et al., 2014a). The female is the only parent who assists the nestlings in handling prey (Newton, 1979; Watson, 2010). Prey selection influences when the nestlings can handle prey unassisted, thus influencing the female time budget (Sonerud et al., 2014a). When the nestlings handle prey unassisted, the female may resume hunting (Newton, 1979), thereby increasing the amount of delivered prey. The reproductive success may be limited by the delivery rate (Davies et al., 2012), and in earlier studies, other single-prey loaders have shown an increase in delivery rate with nestling age (Blondel et al., 1991; Barba et al., 2009; Steen et al., 2012).

When the golden eagles' nestlings manage to tear prey apart, they may handle prey unassisted (Watson, 2010). In common with adult raptors, the nestlings may have extended handling times (cf. Slagsvold & Sonerud, 2007). The nestlings hatch asynchronously, which results in size and development differences between the nestlings (Watson, 2010). Consequently, the largest nestling often harasses or kill the smaller one (Cramp, 1980). This may influence the nestlings' behaviour when handling prey.

The golden eagle's diet and breeding behaviour have not been studied largely using video monitoring. The use of video monitoring can reveal uncommon prey species and an improved estimate of the breeding diet, in addition to behaviour at the nest. I investigated the diet and some components of the breeding behaviour of the golden eagle, using video monitoring at one golden eagle's nest during the breeding season. The aim of my study was to 1) determine the diet of the golden eagle during the nestling period by registering delivered prey, 2) determine if prey items are handled prior to delivery at the nest, by plucking, decapitation or being partly eaten, 3) reveal the prey delivery pattern throughout the day, 4) investigate how nestling age influences the amount of delivered prey, which parent delivers prey and prey composition, 5) what affects whether nestlings handle prey unassisted, and lastly, 6) how long, and how the nestlings handle prey, in addition to the net prey mass handled by each of the nestlings.

Materials and method

Study area

This study took place in Innlandet county in southern Norway. The area was within 61°10´-61°60' N, 8°80´-10°60' E (the specific location is confidential). Data were collected at one golden eagle nest during the breeding season. *Landskap – NiN* (2020) categorises the area surrounding the nest as a relatively open valley-landscape beneath the treeline. Common trees in the area are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), in addition to some Birch (*Betula* spp.). The nest was in proximity to open mountainous areas more than 1000 m above sea level, and human settlements in the area were scarce. However, the nest was not far from farmland with grazing ungulates. The nest was located on a ledge in a southwest-facing cliff, about 900 m above sea level, at the border between forest and open alpine landscape. The nestlings were determined to be approximately eight days old when the fieldwork began, based on earlier observations from golden eagles' nests (G.A. Sonerud, personal communication, January 7th, 2021) and development descriptions in Watson (2010). The two nestlings fledged on the 29th of July and the 4th of August. The golden eagles returned to the nest several times after fledging.

Video monitoring

The nest was video monitored to investigate breeding diet and behaviour during the nestling period. The method used for video monitoring is described by Steen (2009). The equipment used consisted of a camera with a wide-angle lens, a mini digital video recorder (mini-DVR) with a video motion detection (VMD) sensor, a 32 giga-byte SD memory card, a solar panel, and a 12V battery. The camera was installed in autumn to avoid disturbing the golden eagles too close to the breeding season. The camera was mounted in an adjacent tree and was connected to the mini-DVR with a 20 m long cable. The mini-DVR was placed beneath the nest at an accessible site. The set-up in the field is also displayed in figure 1. The sensitivity of the VMD sensor was set to five. A 12V battery powered the mini-DVR, and the battery was connected to a south-west facing solar panel to postpone depletion. The battery and mini-DVR were placed in boxes and covered by tarpaulin to protect from harsh weather.

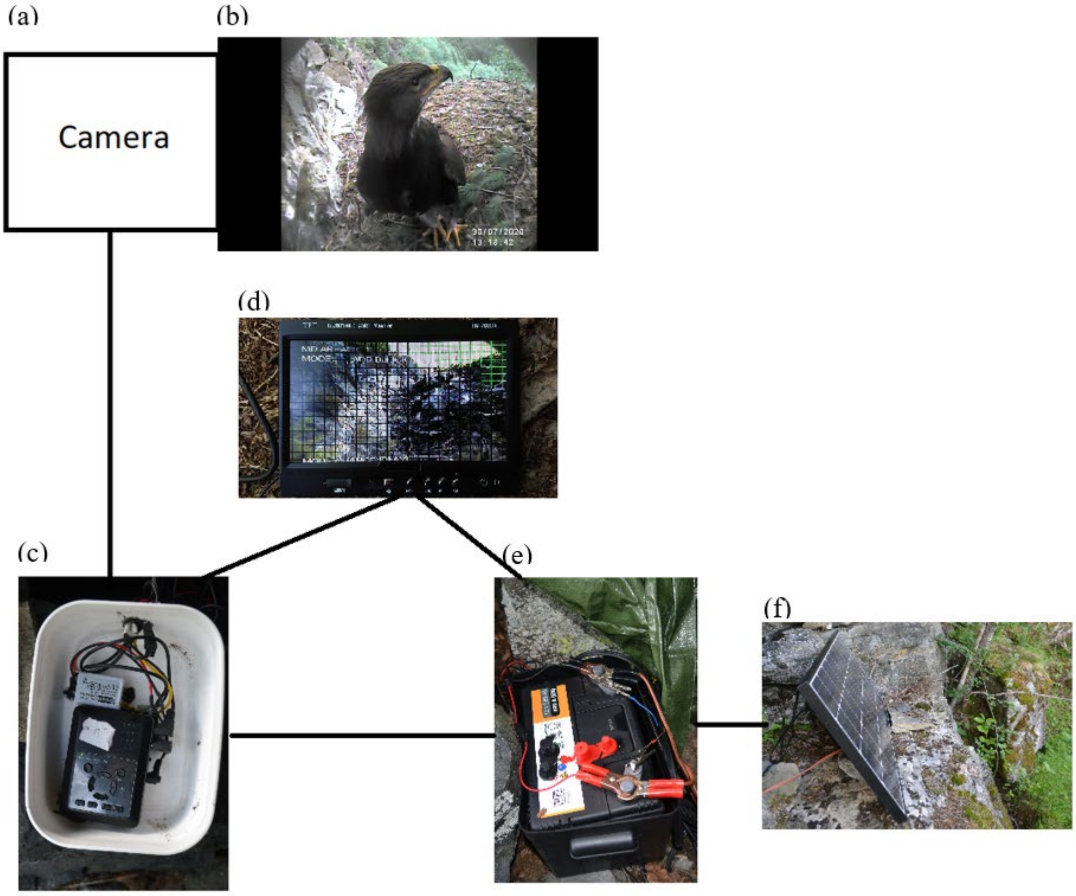


Figure 1. The field set up for video monitoring a golden eagle nest during the breeding season in 2020, where **(a)** represents the camera, **(b)** is a still picture from the video recordings, **(c)** the mini-DVR, **(d)** the portable LCD-screen, **(e)** the battery powering the mini-DVR and the camera and **(f)** the solar panel.

The fieldwork was carried out from the 19th of May to the 29th of August in 2020. The site was visited every three to four days during this period until the last nestling fledged. At each visit, the memory card was changed and the content examined. Additionally, the mini-DVR was inspected, and the picture from the camera was controlled by connecting a portable LCD screen.

The set-up for monitoring the nest presented some challenges. The memory card filled up faster than expected. Consequently, seven days of monitoring were lost. In an attempt to mitigate, the masking was changed two times, which had some impact. Still, how long the memory card's capacity would last was variable and challenging to predict. The camera-angle changed twice due to disturbance from the golden eagles. Additionally, the solar panel did not generate enough power to compensate for the energy used. Therefore, the battery was depleted in mid-July. For eight days, the recording unit went on and off, mostly off at night. The battery was changed as soon as the issue was discovered. Possibly due to the discharged battery, the time on the mini-DVR had shifted. The time was corrected, and all prey deliveries with incorrect time were excluded from the analysis of delivery patterns. The exact time of delivery was not possible to determine for 43 prey items. Still, these deliveries were included when analysing the number of prey and mass delivered per day.

A total of 53 158 video clips which lasted approximately 495 hours in total was collected. The length of the clips recorded ranged from 3 s to 16 m and 55 s. The camera was active for approximately 2 232 hours, and throughout the field period, the recording unit was inactive for less than 10 % of the time. At least five prey items were delivered when the recording unit was inactive. These were discovered when the camera became active and were included in the analysis.

Registering prey delivered at the nest

To determine the golden eagle's breeding diet, all prey items delivered at the nest were registered. The recordings were sorted, and those containing prey deliveries were collected. Further, Microsoft Excel for Microsoft 365 (version 2008) was used to register data. All prey items delivered were identified by watching the video clips frame by frame several times. Prey were identified to the lowest taxonomic class and divided into three groups: bird, mammal, or amphibian. The time of delivery and the delivering parent were also determined. Which of the parents who delivered the prey was usually evident because only the male was ringed. Time of delivery was defined as when the delivering parent's feet hit the nest and was registered to the nearest s. The handler of prey was also determined. If both the female assisted the nestlings when feeding and the nestlings handled the same prey unassisted, it was classified as assisted handling. Furthermore, whether the prey was juvenile and the state upon delivery; decapitated, plucked or partly eaten, were registered. In total, the golden eagles delivered 304 prey items while the nest was monitored. Of these, 274 were determined to both group and either order, family, or species. Another 17 were determined only to a group, and a further 13 were unidentified. Some of the birds determined to thrush (*Turdus* spp.) may potentially have been other passerines of the same size. Twenty-seven of the delivered prey were classified as juvenile prey. There was some uncertainty about the state upon delivery for some prey items, but it was determined for 168 deliveries. The rest of the delivered prey lacked one or several of the categories for state upon delivery.

All delivered prey items were assigned a gross and net mass. Gross mass was the species' average body mass and was acquired from Cramp (1980); Cramp (1983); Cramp (1988); Cramp (1993); Cramp (1994); Frislid & Jensen (1994). Seventeen of the prey items could only be identified as birds. Six of these were assigned the mean gross mass for birds of 181 g. The others were divided into large, medium, and small birds by comparing with the size of the golden eagles. Three birds were determined as large, seven were of medium size, and one bird was small. Gross mass was set to 500 g, 100 g and 30 g, respectively. Of the delivered prey, 13 could not be identified. The gross mass of three of these was determined by comparing the size to the size of the golden eagles. The other 10 were assigned the mean gross mass for prey items of 276 g. The gross mass of 45 of the prey identified to species was determined by comparing them to the golden eagles' size. Of the registered prey, 19 were determined to be one out of two species. Nine of those had the same gross mass for the two possible species. The equation below determined the last one's gross mass:

$$\frac{(\#species\ 1 \times mass\ species\ 1) + (\#species\ 2 \times mass\ species\ 2)}{\#species\ 1 + \#species\ 2}$$

One delivery consisted of 10 thrush nestlings and was likely a collection from several nests. They were all small and were estimated to 10 g each. One *Numenius* was not identified to species and therefore assigned the Eurasian whimbrel's gross mass (*Numenius phaeopus*), as this was the more likely prey (*Artskart [Species maps]*, 2021). The net mass was determined from the state upon delivery. Twenty-four of the delivered prey items were partly eaten prior to delivery. The net mass of these was estimated visually. If a bird was decapitated, 12.9 % of the gross mass was subtracted (Sonerud et al., 2014a). If it could not be determined whether a bird was decapitated, the net mass equalled gross mass.

Registering handling by the nestlings

When all prey items had been identified, the prey handling by the nestlings was registered. The method used to register handling time is also described in Steen (2010); Sonerud et al. (2013); Sonerud et al. (2014a); Sonerud et al. (2014b). Handling time was measured to the nearest s and included preparation, partitioning, and feeding. If one nestling monopolised the prey, the definition of handling start was when the nestling was bending down to tear off the first piece. If the nestling swallowed the prey whole, handling started when the nestling received the prey item from the parent or picked it up. If the two nestlings shared, the start of handling was defined when the nestlings grabbed the prey. Pauses in handling were defined as stop in handling for more than 5 s and were excluded from the net handling time. Also, if sibling fights were possible to separate from feeding, the time was excluded from gross handling time. The definition of end in handling was when the item was consumed entirely or abandoned. If the item was swallowed whole, handling ended when the swallowing movements ended. In some cases, the handling time was separated into several bouts. Handling time was divided into bouts if the item was abandoned, or the attention was diverted from the item before the nestling finished handling, and the nestling resumed other activities. The number of bouts was registered. Gross handling time was registered for 174 of the delivered prey, and net handling time was registered for 130 of those.

In some cases, handling time was excluded from the analysis. It was impossible to register handling time for 58 prey items because the nestling handled the prey out of sight. Especially the smallest nestling established a habit of handling behind the camera. Additionally, handling time was not included if it was unclear which prey item was handled, which accounted for six prey items. In one case, the smallest nestling moved out of sight with only scraps left from one small prey. Handling time for this prey was included.

The video recordings of handling time were not continuous. To account for this, the length of lapses between successive clips were registered when the nestlings were handling prey. Fifty-one percent of the lapses were shorter than 10 s, and the lapses ranged from 1 to 522 s. If the nestling's activity had changed after the lapse, the net handling time was excluded. All handling times were divided into four categories. Category 1: No deviations when handling, or lapse between clips being shorter than 6 s. Lapses up to 5 s were acceptable, as the length of a pause had to be more than 5 s to be registered. Category 2: Nestling partly out of sight when handling, or handling with the back towards the camera. Category 3: The length of the lapse between clips ranged from 6 to 30 s. Category 4: The lapse between the clips was longer than 30 s. Seventy-eight of the handling times were placed in category 1, 16 in category 2, 48 in category 3, and 31 handling times in category 4. If the handling time fitted into more than one category, the highest category was assigned.

I also registered which nestling, or both, handled the prey item, if the item was plucked, and if it was swallowed whole. Additionally, I registered how much each of the nestlings handled. When one nestling monopolised the prey, the handled proportion was registered to 100 % of the net prey mass. If both nestlings handled a prey, the proportion was divided equally between the nestlings.

The method used for registering handling times may be vulnerable to observer drift, particularly because only one observer was used. Therefore, the handling time for the first prey from the previous week was re-watched at the beginning of every week. Only the first bout was re-watched. The differences between the first and second observation ranged from 0 to 5 s for gross handling time and 3 to 6 s for net handling time.

Statistical analyses

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020) and the statistical significance level was set to α = 0.05 for all analyses. For the data preparation and statistical analysis in R, I used the packages 'tidyverse' (Wickham et al., 2019), 'rsq' (Dabao, 2021), 'aod' (Lesnoff & Lancelot, 2012) and 'AICcmodavg' (Mazerolle, 2020). Figures were created in R, using the base functions and the packages 'plot3D' (Soetaert, 2019) and 'ggplot2' (Wickham, 2016).

To reveal the golden eagles' diel prey delivery pattern, I analysed the prey delivery pattern in relation to the time of the day using logistic regression. Each day in the study period was divided into 24 hour blocks with the outcome prey delivery or not in each hour block. The outcome was used as the response variable and time of the day as the explanatory variable. The analysis was carried out using the cosine curve fitting method, and the candidate models are presented in Appendix A. The candidate models were evaluated using Akaike's information criterion, and the model with the lowest AIC was selected as the best fit. The curve from the best fit model was compared to the midline estimating statistic of rhythm, MESOR. The MESOR defines the mean expected delivery rate if deliveries are random. When the curve's confidence interval was higher or lower than the MESOR, it was considered as a significant deviation from MESOR.

I wanted to determine if any of the categories of prey handling significantly impacted the estimated gross and net handling time and thus should be excluded from further analyses of handling time. All unassisted handling of prey by the nestlings had been divided into four categories. Two models were tested to predict the influence of these categories on handling time (Appendix B). The linear regression models included gross or net handling time as the response variable, and the handling category and the net prey mass as explanatory variables. The gross and net handling time and the net prey mass were log10 transformed to achieve normal distribution. I included net prey mass to account for differences in handling time due to prey size. Category 3 and 4, which included handling times with lapses longer than 6 s between successive clips, significantly affected both gross and net handling time. Prey handling in category 3 and 4 were therefore excluded from analyses of gross and net handling time.

Further, I wanted to examine what affected prey handling prior to delivery, the influence of nestling age, what affected if the nestlings handled prey unassisted, the nestlings' handling time and how the nestlings were handling prey delivered at the nest. I created several generalised linear models, with binomial, poisson or normal distribution, to test the effect of potential explanatory variables. The response variables and potential explanatory variables are presented in appendix C. In the models with gross prey mass, gross handling time and net handling time as the response variables, the response variables and net prey mass were log10 transformed to achieve normal distribution. The candidate models were tested using Akaike's information criterion to select the best fit model (Akaike, 1974). The candidate models included explanatory variables together and apart, and some interactions were included. If the difference in AIC-values between candidate models was below two, the model with the lowest AIC was not considered substantially better (Burnham & Anderson, 2004). Therefore, if ΔAIC was below two, the most parsimonious model was selected as the most supported model. The most parsimonious model was the model with the least number of parameters (K). The most supported model was tested further as a generalised linear model to explain variation in the response variable. Additionally, the models in Appendix D were tested as generalised linear models and not using AIC, as I only wanted to test the effect of one explanatory variable, the nestling age. The value for R^2 was calculated for all linear regression models, meaning the generalised linear models with normal distribution. The R^2 described in Nagelkerke (1991) was calculated for the logistic and poisson regression models, meaning the generalised linear models with binomial or poisson distribution, respectively.

Additionally, I wanted to test if there were differences in net prey mass handled by each of the two nestlings, and I performed a Welsh's unequal variances t-test. I excluded prey items handled by both nestlings and only included prey handled unassisted by the nestlings until the largest nestling fledged.

Results

Prey delivered at the nest

During the monitoring, the golden eagles delivered 304 prey items at their nest, distributed on at least 20 different prey species (Table 1). Of all delivered prey items, 88.5 % were birds, 6.9 % were mammals, 0.3 % were amphibians, and 4.3 % were unidentified. Thrushes were the most numerous prey and accounted for 57.9 % of all items. Counting both willow ptarmigan (*Lagopus lagopus*) and potential rock ptarmigan (*Lagopus muta*), the second most numerous prey were ptarmigans (*Lagopus* ssp.), which made up 14.5 % of the diet. The mountain hare (*Lepus timidus*) was the third most abundant prey and accounted for 4.6 % of the delivered items.

The total estimated gross mass delivered at the nest was 83 747 g (Table 1). The estimated gross mass of single prey items ranged from 10 g to 4000 g. The mean gross prey mass was 276 g and the median 100 g. Birds made up 58.0 % of the estimated gross mass, mammals 38.5 %, amphibians 0.02 %, and unidentified prey 3.5 %. In terms of gross mass, the mountain hare was the most important prey and made up 35.8 % of the total delivered prey mass. Secondly, ptarmigans accounted for 25.8 % of the total prey mass and thirdly thrushes for 19.2 %. During the study period, no ungulates were delivered at the nest.

Table 1. Prey recorded delivered at a golden eagle nest during the breeding season in 2020.

	Prey number		Estimated gross body mass (g)			Estimated net body mass (g)		
Prey species	N	%	Per prey	All prey	%	Per prey	All prey	%
Hooded crow (*Corvus cornix*)	2	0.7	500	1000	1.2	500	1000	1.4
Willow ptarmigan (*Lagopus lagopus*)	7	2.3	500	3500	4.2	493 [1]	3450	4.8
Ptarmigan (*Lagopus* spp.)	37	12.2	488 [2]	18050	21.6	416 [3]	15377	21.5
Ptarmigan (*Lagopus* sp.)/Black grouse (*Tetrao tetrix*)	1	0.3	518	518	0.6	414	414	0.6
Curlew/whimbrel (*Numenius* sp.)	1	0.3	400	400	0.5	400	400	0.6
Tit (Paridae spp.)	3	1.0	15	45	0.1	15	45	0.1
Passerine (Passeriformes spp.)	6	2.0	37 [4]	220	0.3	36 [5]	217	0.3
Snipe (*Scolopacidae* sp.)	1	0.3	200	200	0.2	200	200	0.3
Eurasian woodcock (*Scolopax rusticola*)	3	1.0	300	900	1.1	265 [6]	796	1.1
Black grouse (*Tetrao tetrix*)	2	0.7	900	1800	2.1	350 [7]	700	1.0
Western capercaillie (*Tetrao urogallus*)	1	0.3	2000	2000	2.4	2000	2000	2.8
Wood sandpiper (*Tringa glareola*)	1	0.3	60	60	0.1	60	60	0.1
Common greenshank (*Tringa nebularia*)	1	0.3	200	200	0.2	174	174	0.2
Redwing (*Turdus iliacus*)/Song thrush (*Turdus philomelos*)	1	0.3	70	70	0.1	70	70	0.1
Blackbird (*Turdus merula*)	10	3.3	100	1000	1.2	97 [8]	974	1.4
Blackbird (*Turdus merula*)/Ring ouzel (*Turdus torquatus*)	8	2.6	100	800	1.0	100	800	1.1
Song thrush (*Turdus philomelos*)	5	1.6	70	350	0.4	70	350	0.5
Fieldfare (*Turdus pilaris*)	22	7.2	100	2200	2.6	99 [9]	2187	3.1
Thrush indet. (*Turdus* spp.)	129	42.4	90 [10]	11600	13.9	88 [11]	11412	15.9
Ring ouzel (*Turdus torquatus*)	1	0.3	100	100	0.1	100	100	0.1
Unidentified bird	27	8.9	132 [12]	3556	4.2	128 [13]	3452	4.8
Total bird	**269**	**88.5**	**181**	**48569**	**58.0**	**164**	**44178**	**61.7**
Norway lemming (*Lemmus lemmus*)	1	0.3	50	50	0.1	50	50	0.1
Mountain hare (*Lepus timidus*)	14	4.6	2143 [14]	30000	35.8	1586 [15]	22200	31.0
Field vole/Root vole (*Microtus* spp.)	2	0.7	40 [16]	80	0.1	40 [17]	80	0.1
American mink (*Neovison vison*)	3	1.0	600	1800	2.2	600	1800	2.5
Eurasian red squirrel (*Sciurus vulgaris*)	1	0.3	300	300	0.4	300	300	0.4
Total mammal	**21**	**6.9**	**1535**	**32230**	**38.5**	**1163**	**24430**	**34.1**
Common frog (*Rana temporaria*)	1	0.3	20	20	0.02	20	20	0.03
Total amphibian	**1**	**0.3**	**20**	**20**	**0.02**	**20**	**20**	**0.03**
Unidentified prey	13	4.3	225 [18]	2928	3.5	225 [19]	2928	4.1
Total	**304**	**100.0**	**276**	**83747**	**100.0**	**235**	**71557**	**100.0**

[1] Mean estimate, variation 450-500 g
[2] Mean estimate, variation 50-500 g
[3] Mean estimate, variation 50-500 g
[4] Mean estimate, variation 20-100 g
[5] Mean estimate, variation 17-100 g
[6] Mean estimate, variation 235-300 g
[7] Mean estimate, variation 100-600 g
[8] Mean estimate, variation 87-100 g
[9] Mean estimate, variation 87-100 g
[10] Mean estimate, variation 10-100 g
[11] Mean estimate, variation 10-100 g
[12] Mean estimate, variation 20-500 g
[13] Mean estimate, variation 20-500 g
[14] Mean estimate, variation 500-4000 g
[15] Mean estimate, variation 200-4000 g
[16] Mean estimate, variation 30-50 g
[17] Mean estimate, variation 30-50 g
[18] Mean estimate, variation 20-276 g
[19] Mean estimate, variation 20-276 g

Prey handling prior to delivery

Out of the 304 prey items delivered, the eagles had not handled 106 to any degree prior to delivery. Sixty-three prey items could not be scored for any handling prior to delivery, and 86 could be scored for either decapitated, plucked, or partly eaten prior to delivery at the nest. Eighty-six had been handled to some degree, and 12 of these prey items were registered as both decapitated, plucked and partly eaten. Out of the 198 prey items that could be determined to be decapitated or not, 39 (19.7 %) were decapitated. Of the decapitated prey, 87.2 % were birds. Of the birds delivered at the nest, 193 could be determined to be plucked or not. Sixty-nine (32.4 %) of these were plucked prior to delivery. Two hundred twenty of the delivered prey could be determined to be partly eaten prior to delivery or not. Of these, 24 (10.9 %) were partly eaten. Of the ones partly eaten, 75 % were birds.

Factors that could affect whether prey was delivered decapitated or not could be nestling age, gross prey mass and the delivering parent. A variety of models were tested using Akaike's information criterion, and the most supported model with the least number of parameters was identified (Table 2). Model 1 was determined as the most parsimonious model of the most supported ones and was tested further.

Table 2. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting whether a prey was delivered decapitated or not at the golden eagle nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
4	Nestling age + Gross prey mass	3	154.16	0.00	0.41
9	Nestling age + Gross prey mass + Delivering parent	4	155.22	1.06	0.24
1	Nestling age	2	155.57	1.41	0.20
6	Nestling age + Delivering parent	3	156.22	2.06	0.15
5	Nestling age * Gross prey mass	4	156.24	2.08	0.13
7	Gross prey mass + Delivering parent	3	186.28	32.11	0.00
2	Gross mass	2	187.12	32.96	0.00
8	Gross prey mass * Delivering parent	4	188.19	34.02	0.00
3	Delivering parent	2	196.92	42.75	0.00
0		1	198.50	44.34	0.00

The nestling age best predicted whether a prey item was decapitated or not prior to delivery (Table 2). The predicted probability of decapitation decreased significantly as the nestlings grew older (Table 3, Figure 2).

Table 3. Parameter estimates from the most supported logistic regression model (i.e. model 1 in Table 2). The parameters predict the probability of a delivered prey being decapitated before delivered at the golden eagle nest. R^2=0.32.

	Estimate	Std. error	z-value	p	
Intercept	2.256	0.618	3.650	0.0003	***
Nestling age	-0.075	0.013	-5.826	< 0.0001	***

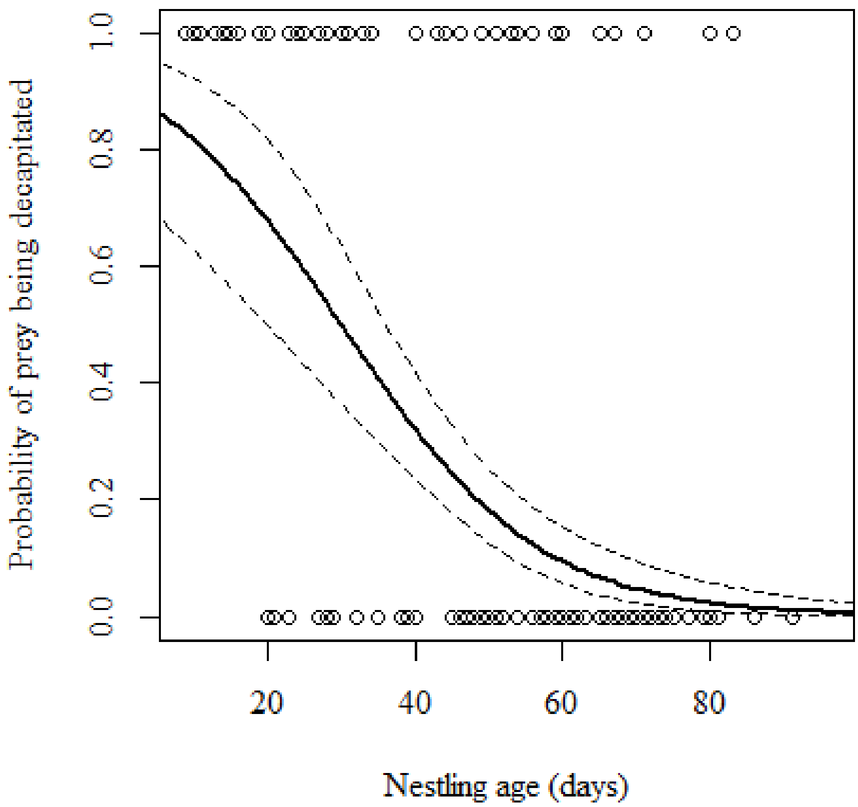


Figure 2. The predicted probability of a prey item delivered at the golden eagle nest being decapitated prior to delivery. The curve represents the predicted probability of a prey being decapitated in relation to nestling age, as estimated by the logistic regression model in Table 3. The dashed lines represent the upper and lower 95 % confidence intervals. Each circle represents a delivered prey item and shows whether it was decapitated (1.0) or not (0.0) prior to delivery.

Factors potentially influencing whether a bird was delivered plucked at the nest were nestling age, gross prey mass and the delivering parent. The best fit model was identified based on Akaike's information criterion. As shown in table 4, model 7 was the best fit and was tested further.

Table 4. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting whether a prey was delivered plucked or not at the golden eagle nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
7	Gross prey mass + Delivering parent	3	224.11	0.00	0.73
8	Gross prey mass * Delivering parent	4	226.00	1.89	0.79
9	Gross prey mass + Delivering parent + Nestling age	4	226.15	2.04	0.26
2	Gross prey mass	2	237.83	13.72	0.00
6	Delivering parent + Nestling age	3	239.27	15.16	0.00
4	Gross prey mass + Nestling age	3	239.78	15.67	0.00
5	Gross prey mass * Nestling age	4	241.12	17.01	0.00
3	Delivering parent	2	241.43	17.32	0.00
1	Nestling age	2	252.07	27.96	0.00
0		1	253.68	29.57	0.00

The model including gross prey mass and the delivering parent was the best fit and predicted whether a bird was delivered plucked or not at the nest (Table 4). The predicted probability of a bird being plucked increased with gross prey mass (Table 5). Also, the predicted probability of a bird being plucked prior to delivery was marginally non-significantly higher if the male delivered it rather than the female.

Table 5. Parameter estimates from the best fit logistic regression model (i.e. model 7 in Table 4). The parameters predict the probability of a delivered prey being plucked in advance of delivery at the golden eagle nest. $R^2 = 0.22$.

	Estimate	Std. error	z-value	p	
Intercept	-1.772	0.370	-4.779	< 0.0001	***
Gross prey mass	0.003	0.001	4.011	< 0.0001	***
Delivering parent (Male)	0.630	0.368	1.712	0.0869	

Factors that could affect whether a prey was partly eaten before delivery could be nestling age, gross prey mass and the delivering parent. A variety of models were tested with Akaike's information criterion, and the best model identified (Table 6). The best fit was model 9, which was tested further.

Table 6. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting if a prey is partly eaten before delivery at the golden eagle nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
9	Nestling age + Gross prey mass + Delivering parent	4	123.05	0.00	0.76
4	Nestling age + Gross prey mass	3	125.48	2.43	0.23
5	Nestling age * Gross prey mass	4	125.60	2.55	0.17
7	Gross prey mass + Delivering parent	3	132.28	9.23	0.01
8	Gross mass * Delivering parent	4	133.52	10.48	0.00
1	Nestling age	2	134.21	11.16	0.00
6	Nestling age + Delivering parent	3	134.31	11.26	0.00
2	Gross prey mass	2	135.06	12.01	0.00
3	Delivering parent	2	152.43	29.38	0.00
0		1	153.65	30.60	0.00

Whether prey was partly eaten before delivery was best explained by the model including nestling age, gross prey mass and the delivering parent (Table 6). The predicted probability of a prey being delivered partly eaten decreased significantly with nestling age and increased significantly with gross prey mass. Also, the predicted probability of a prey being delivered partly eaten was marginally non-significantly higher if the male delivered the prey than if the female delivered the prey (Table 7).

Table 7. Parameter estimates from the best fit logistic regression model (i.e. model 9 in Table 6). The parameters predict the probability of a prey being partly eaten prior to delivery at the golden eagle nest. R^2=0.31.

	Estimate	Std. error	z-value	p	
Intercept	-1.3865	0.8721	-1.590	0.1119	
Nestling age	-0.0436	0.0134	-3.245	0.0012	**
Gross prey mass	0.0012	0.0004	3.175	0.0015	**
Delivering parent (Male)	1.1680	0.6653	1.756	0.0792	

Diel delivery pattern

During the study period, the parents delivered prey in 21 out of the 24 hour blocks of the day. The earliest delivery was recorded at 03:27, and the latest at 23:27, which was 2 hours 6 minutes after and 1 hour 54 minutes before solar midnight, respectively. The model best predicting the eagles' diel delivery pattern was selected using Akaike's information criterion (Appendix A). Model 1 was identified as the best fit and was tested further. The eagles' delivery pattern had one peak around 12:00 with the highest predicted probability of a prey being delivered (Table 8, Figure 3). The predicted probability of a prey delivery was significantly higher than randomly expected between 09:00 and 16:00 and significantly lower between 19:00 and 06:00.

Table 8. Parameter estimates from the best fit logistic regression model (i.e. model 1 in Appendix A). The parameters predict the probability of a prey being delivered at the golden eagle nest through the day. R^2=0.15.

	Estimate	Std. error	z-value	p	
Intercept	-2.139	0.099	-21.675	< 0.0001	***
I(cos(2*pi*Hour/24))	-1.342	0.135	-9.930	< 0.0001	***
I(sin(2*pi*Hour/24))	-0.175	0.117	-1.504	0.133	

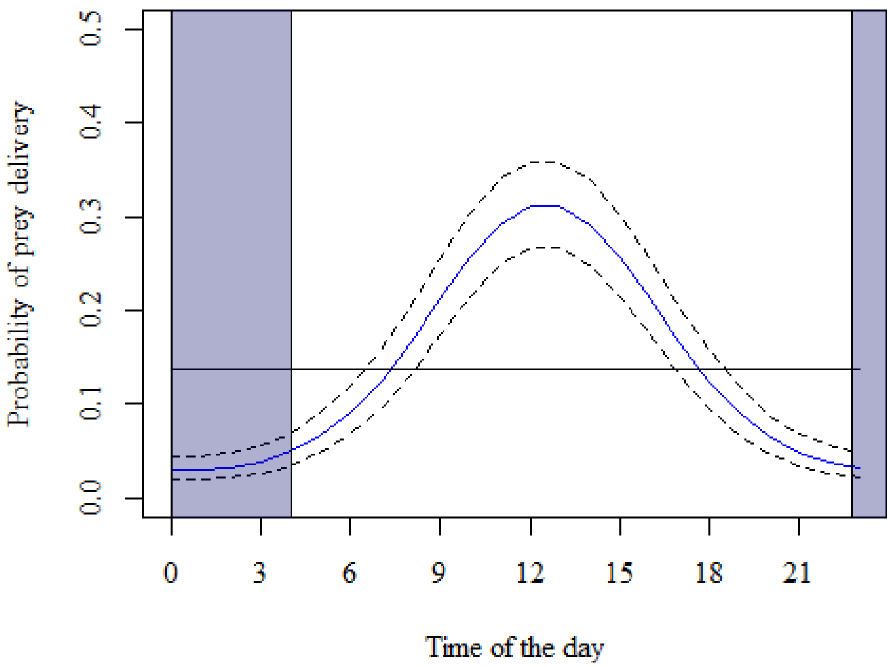
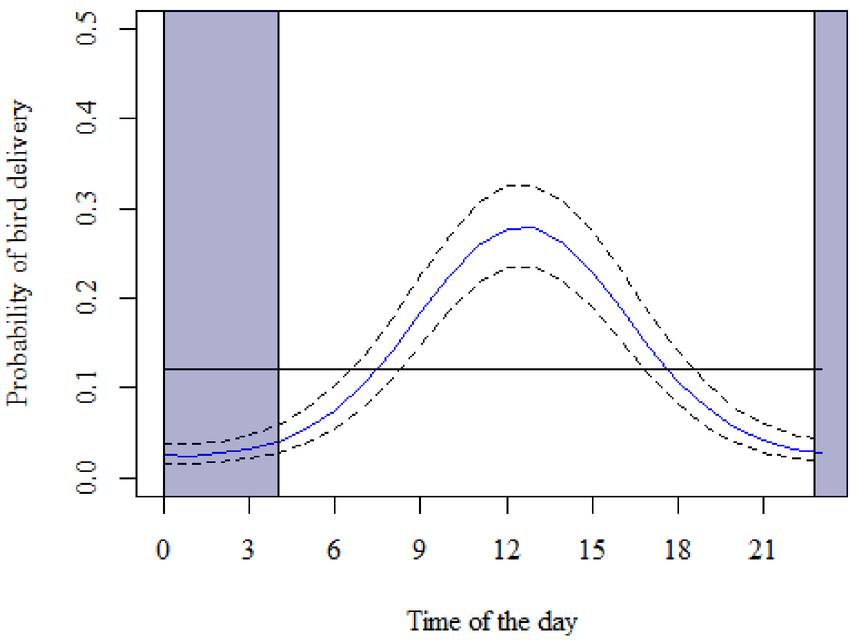


Figure 3. The predicted probability of the golden eagles delivering a prey item at the nest in relation to the time of the day during the breeding season, represented by the blue line. The dashed lines represent the 95 % confidence interval and the horizontal line the midline estimating statistic of rhythm (MESOR). The purple boxes define the hours between sunset and sunrise.

The curve's shape was the same for all prey and when divided into mammals and birds (Figure 3, Figure 4). However, mammals had a lower peak and a considerably lower predicted probability of being delivered. Additionally, the predicted probability of a mammal being delivered was only significantly higher than randomly expected between 09:00 and 13:00.

(a)



(b)

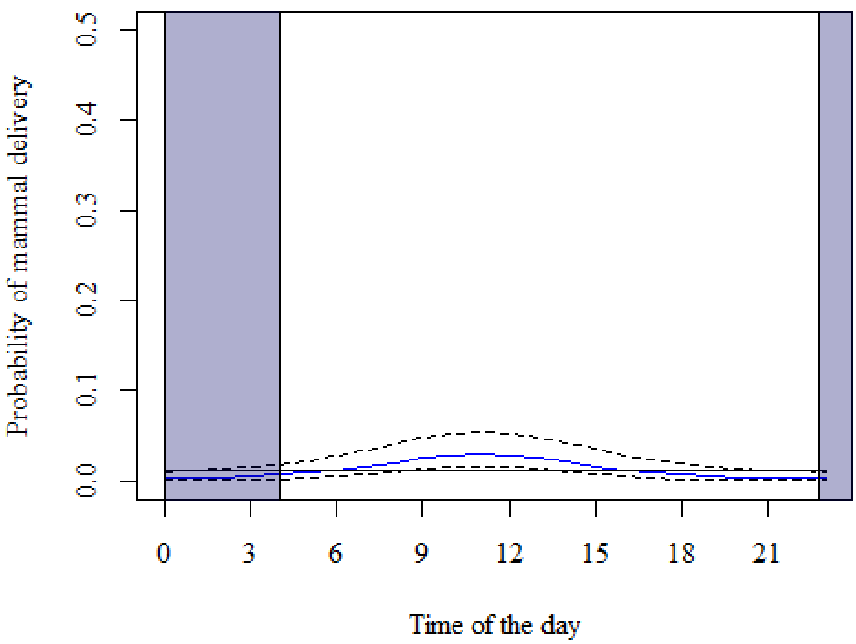


Figure 4. The predicted probability of the golden eagles delivering a bird **(a)** and a mammal **(b)** at the nest in relation to the time of the day during the breeding season, represented by the blue line. The dashed lines represent the 95 % confidence interval and the horizontal line the midline estimating statistic rhythm (MESOR). The purple boxes define the hours between sunset and sunrise.

Influence of nestling age

Of the 304 prey items delivered during the study period, the highest number delivered in one day was 20 individuals. On that day, the nestlings were 58 days old. There were 11 days when the golden eagles delivered no prey at the nest. Nestling age significantly affected the number of prey items delivered each day (Table 9). The predicted number of prey items delivered each day increased as the nestlings grew older. Additionally, the last days before both nestlings fledged, there was a decrease in the number of prey items delivered per day (Figure 5).

Table 9. Parameter estimates of the poisson regression model predicting the number of prey items delivered at the golden eagle nest each day during the breeding season. R^2=0.30.

	Estimate	Std. error	z-value	p	
Intercept	0.653	0.149	4.385	< 0.0001	***
Nestling age	0.013	0.003	5.267	< 0.0001	***

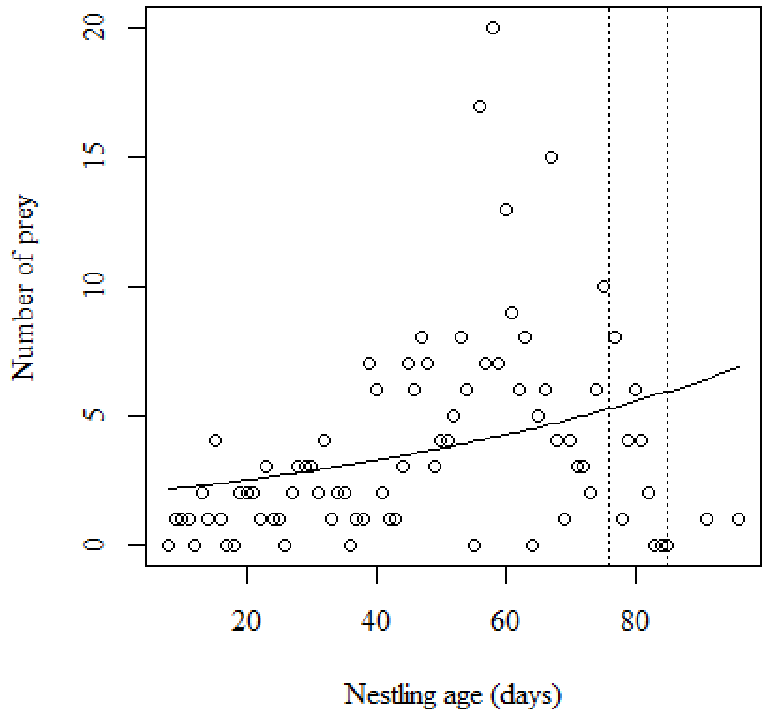


Figure 5. The number of prey items delivered at the golden eagle nest each day during the breeding season. The curve represents the predicted number of prey delivered in relation to nestling age, as estimated by the poisson regression model in Table 9. The dotted vertical lines indicate when each of the two nestlings fledged. Each circle represents the number of prey delivered per day.

The predicted number of prey items delivered each day increased with the nestling age. Still, nestling age did not affect the prey mass delivered each day (Table 10, Figure 6). The model predicted no increase or decrease in the total mass delivered each day as the nestlings grew older.

Table 10. Parameter estimates from the linear regression model predicting the total net prey mass delivered each day at the golden eagle nest during the breeding season. R^2=0.0008.

	Estimate	Std. error	t-value	p	
Intercept	896.644	202.984	4.417	< 0.001	***
Nestling age	-0.957	3.847	-0.249	0.804	

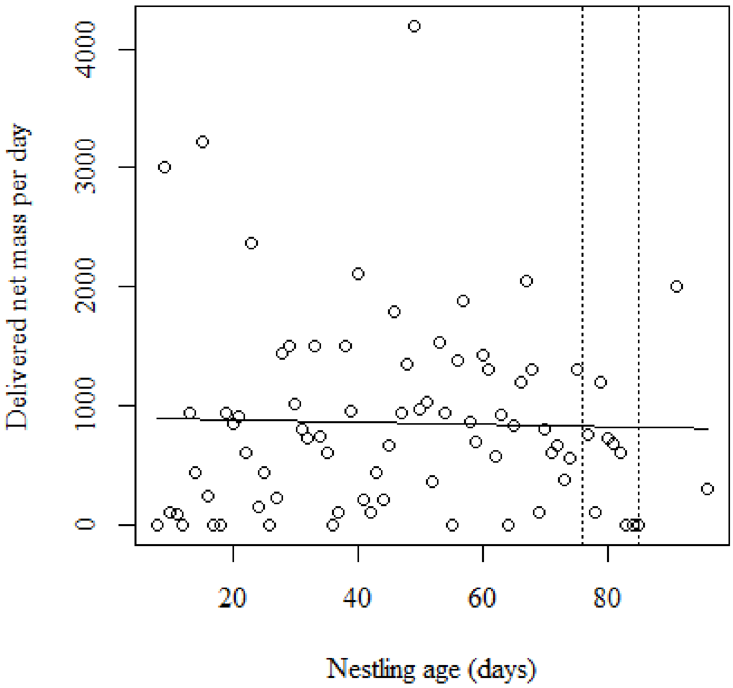


Figure 6. The total net mass delivered at the golden eagle nest each day during the breeding season. The solid line represents the predicted mass delivered in relation to nestling age, as estimated by the linear regression model in Table 10. The dotted vertical lines indicate when each of the two nestlings fledged. Each circle represents the delivered net prey mass per day.

The delivering parent was identified for 285 of the 304 delivered prey items. The male delivered 69.8 % of the prey items. The age of the nestlings did not affect which parent delivered a prey item (Table 11).

Table 11. Parameter estimates from the logistic regression model predicting the probability of the delivering parent at the golden eagle nest being the male. R^2=0.0006.

	Estimate	Std. error	z-value	p	
Intercept	0.987	0.430	2.291	0.022	*
Nestling age	-0.003	0.008	-0.358	0.720	

Factors potentially influencing the gross mass of a delivered prey were the delivering parent and nestling age. The best fit model was selected based on Akaike's information criterion (Table 12). Model 4 was the best fit model and was tested further.

Table 12. The model selection output of Akaike's information criterion, used to identify the linear regression model with the factors best predicting the gross mass of a prey delivered at the golden eagle nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
4	Delivering parent * Nestling age	5	373.84	0.00	0.85
3	Delivering parent + Nestling age	4	377.36	3.52	0.15
1	Nestling age	3	386.19	12.36	0.00
2	Delivering parent	3	406.39	32.56	0.00
0		2	430.33	56.50	0.00

The gross prey mass was best explained by the model including the sex of the delivering parent, the nestlings' age, and the interaction between the sex of the delivering parent and the nestling age (Table 12). The predicted gross prey mass decreased significantly if the delivering parent were the male rather than the female (Table 13, Figure 7). The predicted gross mass of prey decreased significantly as the nestlings grew older. There was a significant interaction between the sex of the delivering parent and the nestling age. As the nestlings grew older, the male had a higher predicted probability of delivering prey with a higher gross mass than if the female delivered the prey.

Table 13. Parameter estimates from the best fit linear regression model (i.e. model 4 in Table 12) of variables affecting the gross mass of prey items delivered at the golden eagle nest. R^2=0.22.

	Estimate	Std. error	t-value	p	
Intercept	2.969	0.158	18.821	< 0.0001	***
Delivering parent (Male)	-0.529	0.192	-2.748	0.0064	**
Nestling age	-0.014	0.003	-5.256	< 0.0001	***
Delivering parent (Male) * Nestling age	0.008	0.003	2.359	0.0190	*

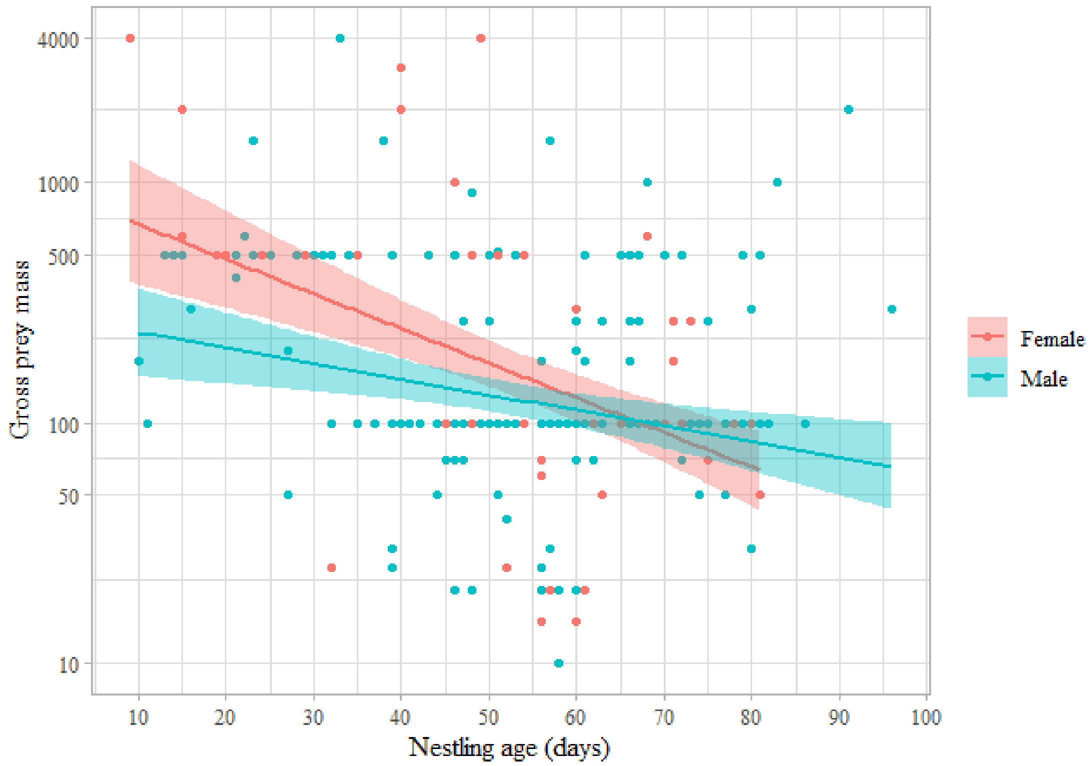


Figure 7. The predicted gross mass of prey as a function of nestling age for each of the golden eagle parents. The two lines represent the predicted gross mass of delivered prey, as estimated by the linear regression model in Table 13. The coloured areas around the solid lines represent the 95 % confidence intervals. Each dot represents a delivered prey item.

Thrushes were the most numerous prey throughout the study period. Factors potentially influencing if a delivered prey item were a thrush or another prey type were the delivering parent and the nestling age. Akaike's information criterion identified model 4 as the model with the best fit (Table 14). Model 4 was tested further.

Table 14. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting the probability of a delivered prey at the golden eagle nest being a thrush.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
4	Delivering parent * Nestling age	4	362.41	0.00	0.77
3	Delivering parent + Nestling age	3	364.79	2.38	0.23
1	Nestling age	2	378.18	15.77	0.00
2	Delivering parent	2	392.89	30.48	0.00
0		1	415.84	53.43	0.00

If a delivered prey were a thrush or not was best explained by the model including the sex of the delivering parent, the nestlings' age, and the interaction between these, which was the same explanatory variables for gross prey mass (Table 12, Table 14). The predicted probability of a prey being a thrush increased significantly as the nestlings grew older and if the male delivered the prey rather than the female (Table 15, Figure 8). Additionally, the interaction between the sex of the delivering parent and nestling age was significant. As the nestlings grew older, the male had a lower increase than the female in the predicted probability of delivering a thrush.

Table 15. Parameter estimates of the best fit logistic regression model (i.e. model 4 in Table 14) predicting the probability of a delivered prey at the golden eagle nest being a thrush. R^2=0.25.

	Estimate	Std. error	z-value	p	
Intercept	-3.622	1.012	-3.579	0.0004	***
Delivering parent (Male)	2.351	1.133	2.075	0.0380	*
Nestling age	0.069	0.018	3.957	< 0.0001	***
Delivering parent (Male) * Nestling age	-0.039	0.020	-1.979	0.0478	*

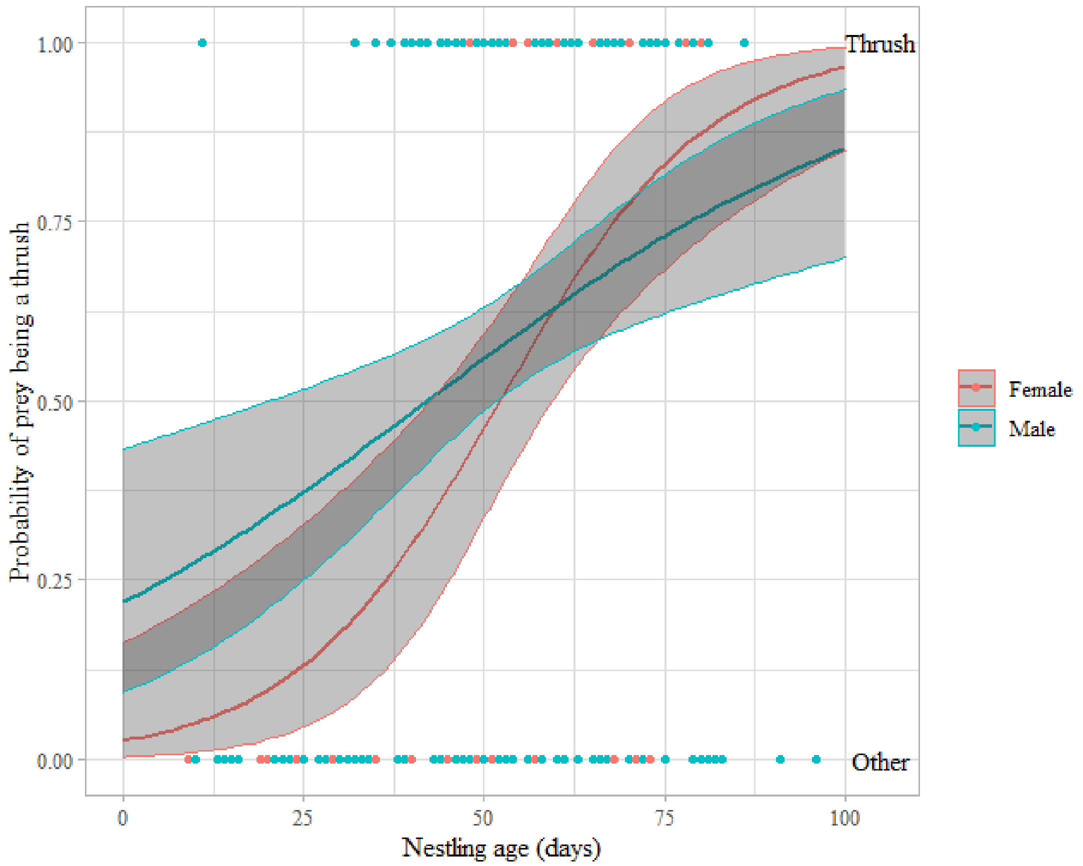


Figure 8. The predicted probability of a delivered prey at the golden eagle nest being a thrush in relation to nestling age when delivered by the male or the female, as estimated by the logistic regression model in Table 15. The bold lines inside the grey area represent the estimated probability, and the grey area the 95 % confidence intervals. Each dot represents a delivered prey item and shows whether it was a thrush (1.0) or another prey (0.0).

The proportion of the various prey categories changed as the nestlings grew older (Figure 9). Birds were the most numerous prey throughout all three periods, but mammals contributed considerably to the gross prey mass. Until the nestlings were 32 days old, ptarmigans accounted for 57.5 % of all prey by number and 49.7 % of the total gross prey mass. In the same period, thrushes made up only 7.5 % of all prey by number. In the middle period, when the nestlings were between 33 and 64 days old, thrushes accounted for 65.1 % of all prey by number. In this period, mountain hares accounted for 43.7 % of the gross prey mass. The composition of prey in the last period when the nestlings were between 65 and 96 days old was quite similar to the middle period.

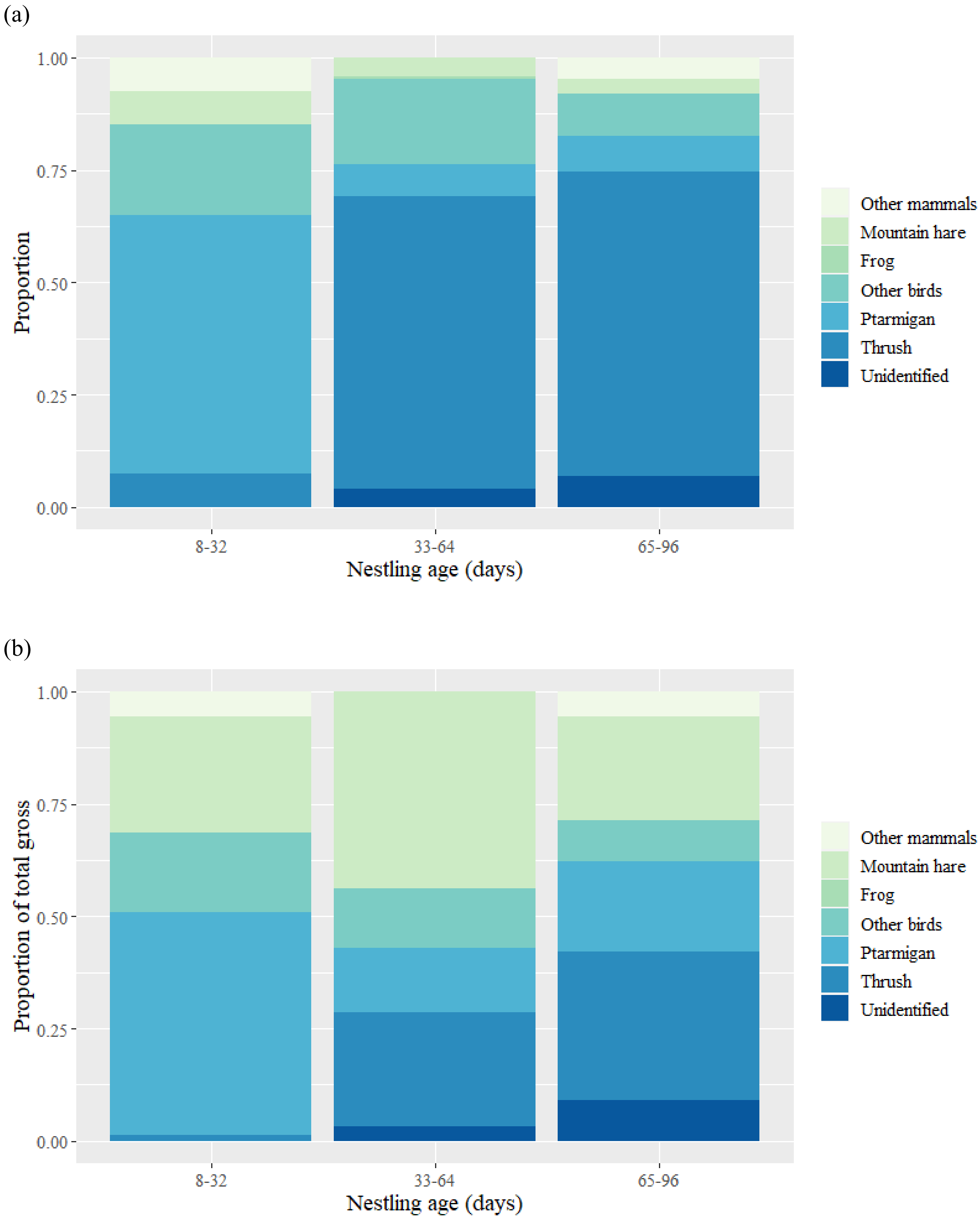


Figure 9. The proportion of prey types delivered at the golden eagle nest in relation to nestling age, calculated by number **(a)** and total gross mass **(b)**. Note that there is no data on delivered prey before the nestlings were eight days old.

Nestlings handling unassisted

For 295 prey delivered at the nest, it could be confirmed whether the nestlings handled the prey unassisted or the female assisted in prey handling. The female assisted the nestlings in handling 64 (21.7 %) of the prey items, and the nestlings handled 231 (78.3 %) of the prey unassisted. Of the prey handled unassisted by the nestlings, 91.8 % were birds. The proportion was lower for prey handled assisted, where 79.7 % were birds. Factors that could influence if the female assisted in handling were nestling age, net prey mass and gross prey mass. Akaike's information criterion was checked for potential models predicting unassisted handling, and the most parsimonious model of the most supported ones was identified (Table 16). Model 4 was identified as the best model and therefore tested further.

Table 16. The model selection output of Akaike's information criterion, used to identify the logistic regression model best predicting if the female golden eagle assisted her nestlings in prey handling or not at the nest during the breeding season.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
5	Nestling age * Net prey mass	4	92.32	0.00	0.36
7	Nestling age * Gross prey mass	4	92.38	0.06	0.35
4	Nestling age + Net prey mass	3	94.06	1.74	0.15
6	Nestling age + Gross prey mass	3	94.09	1.77	0.15
1	Nestling age	2	122.11	29.79	0.00
2	Net prey mass	2	210.45	118.12	0.00
3	Gross prey mass	2	211.52	119.20	0.00
0		1	311.57	219.25	0.00

The female monopolised prey handling until the nestlings were 27 days old. After that, there was a gradual shift towards the nestlings handling prey unassisted. When the nestlings were 40 days old, the predicted probability of unassisted handling was slightly more than 50 %. Between the age of 43 and 58 days, the nestlings handled 86.8 % of the prey unassisted. After the nestlings were 58 days old, the female did not assist in any handling of prey. Whether the nestlings handled prey unassisted or not were best explained by the model including nestling age and net prey mass (Table 16). The predicted probability of unassisted prey handling decreased significantly with increasing net prey mass and increased significantly as the nestlings grew older (Table 17, Figure 10).

Table 17. Parameter estimates from the most supported logistic regression model (i.e. model 4 in Table 16) for the probability of the nestlings handling prey unassisted by the female at the nest during the golden eagles' breeding season. $R^2=0.76$.

	Estimate	Std. error	z-value	p	
Intercept	-6.081	1.372	-4.433	< 0.0001	***
Nestling age	0.187	0.030	6.162	< 0.0001	***
Net prey mass	-0.006	0.002	-3.716	0.0002	***

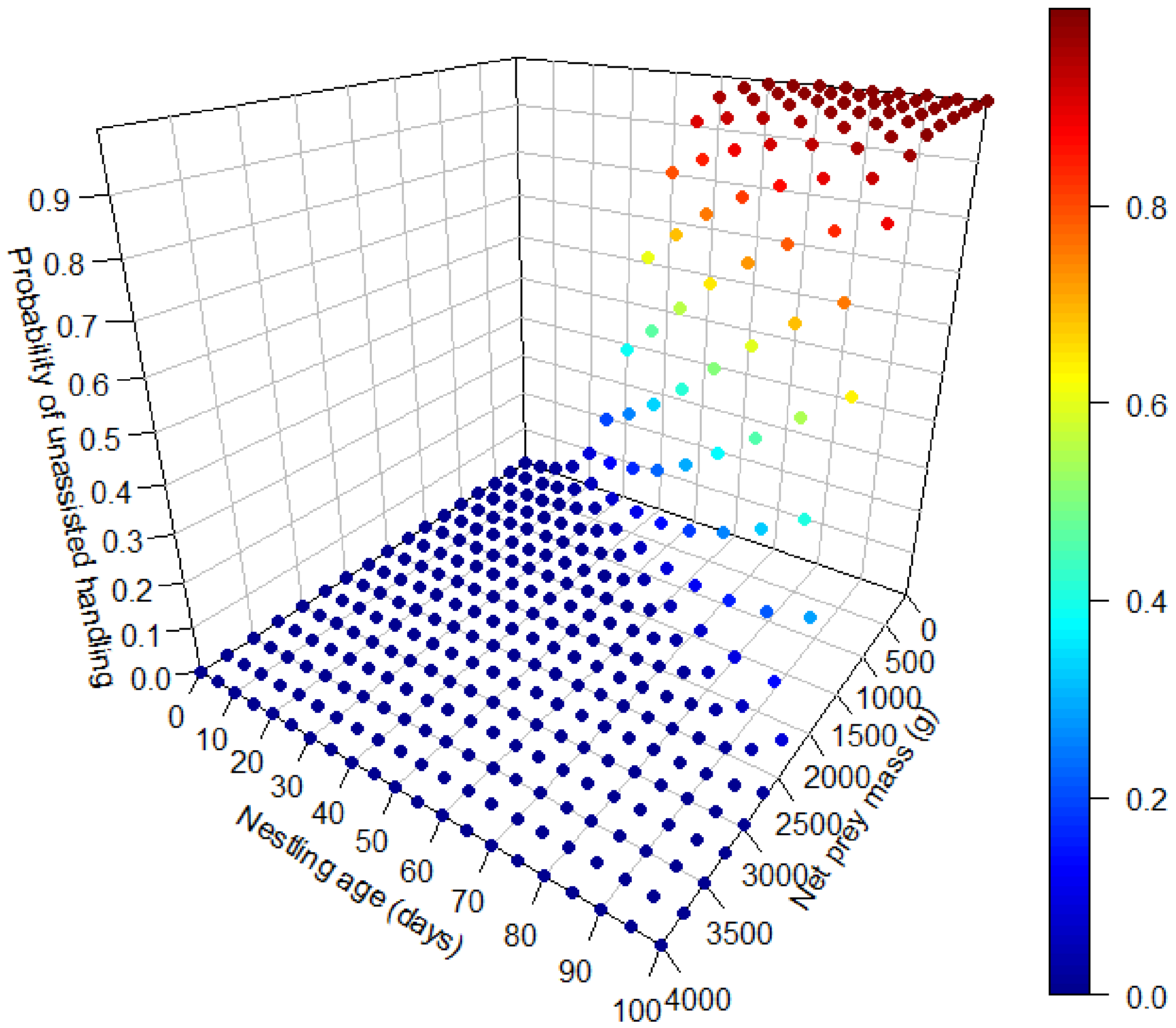


Figure 10. The predicted probability of the nestlings handling prey unassisted by the female at the nest during the golden eagles' breeding season. The predicted probability of unassisted handling is presented as a function of nestling age and net prey mass, as estimated by the logistic regression model in Table 17.

Nestlings handling prey

The nestlings' gross handling time for a prey item ranged from 6 s to 68 minutes 51 s. The mean gross handling time was 4 minutes 35 s, and the median was 3 minutes 3 s. For prey with a net mass of 100 g, the mean handling time was 5 minutes 35 s, and the median was 4 minutes 21 s. Factors that could affect gross handling time were which of the two nestlings that handled the prey or both, the net prey mass, and the age of the nestlings. The best fit model was identified using Akaike's information criterion, and model 4 was tested further (Table 18).

Table 18. The model selection output of Akaike's information criterion, used to identify the linear regression model with the factors best predicting the length of the golden eagle nestlings' gross handling time of prey at the nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
4	Nestling ID + Net prey mass	5	142.27	0.00	0.43
7	Nestling ID + Net prey mass + Nestling age	6	142.79	0.52	0.33
2	Net prey mass	3	144.29	2.02	0.16
6	Net prey mass + Nestling age	4	145.57	3.30	0.08
1	Nestling ID	4	188.30	46.02	0.00
5	Nestling ID + Nestling age	5	190.46	48.19	0.00
0		2	193.01	50.74	0.00
3	Nestling age	3	194.64	52.36	0.00

The gross handling time was influenced by which of the two nestlings handled the prey or both and the net prey mass (Table 18). Compared with the cases when only the largest or the smallest nestling handled prey, the predicted gross handling time was significantly longer when both nestlings handled a prey item (Table 19). Furthermore, the predicted gross handling time increased significantly as the net prey mass increased.

Table 19. Parameter estimates from the best fit linear regression model (i.e. model 4 in Table 18). The parameters predict the gross handling time by the golden eagle nestlings of a delivered prey at the nest. R^2=0.46.

	Estimate	Std. error	t-value	p	
Intercept	0.137	0.246	0.556	0.579	
Nestling ID (Both)	0.593	0.262	2.267	0.026	*
Nestling ID (Small)	-0.093	0.122	-0.757	0.451	
Net prey mass	1.052	0.135	7.771	< 0.0001	***

The net handling time of the nestlings ranged from 6 s to 64 minutes 56 s. The mean net handling time was 4 minutes 16 s and was 19 s shorter than the mean gross handling time. The median for the net handling time was 2 minutes 51 s. For a prey with a net mass of 100 g, the mean net handling time was 5 minutes 12 s, and the median 4 minutes 7 s. Factors that could potentially affect net handling time were which of the two nestlings handled the prey or both, the net prey mass, and the nestling age. The best model for explaining the length of net handling time was selected using Akaike's information criterion (Table 20). Model 2 was the most parsimonious model of the most supported ones and were tested further.

Table 20. The model selection output of Akaike's information criterion, identifying the linear regression model with the factors best predicting the length of the golden eagle nestlings' net handling time of prey at the nest.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
4	Nestling ID + Net prey mass	5	133.36	0.00	0.43
7	Nestling ID + Net prey mass + Nestling age	6	134.21	0.85	0.28
2	Net prey mass	3	134.97	1.61	0.19
6	Net prey mass + Nestling age	4	136.50	3.14	0.09
1	Nestling ID	4	175.53	42.18	0.00
5	Nestling ID + Nestling age	5	177.76	44.40	0.00
0		2	181.02	47.66	0.00
3	Nestling age	3	182.72	49.37	0.00

The nestlings' net handling time was best explained by the net prey mass (Table 20). The predicted length of net handling time increased significantly with the prey mass (Table 21).

Table 21. Parameter estimates from the most supported linear regression model (i.e. model 2 in Table 20). The parameters predict the net handling time by the golden eagle nestlings of a delivered prey at the nest. R^2=0.42.

	Estimate	Std. error	t-value	p	
Intercept	0.075	0.251	0.298	0.766	
Net prey mass	1.074	0.136	7.919	< 0.0001	***

Of the 231 prey items registered as handled by the nestlings, 29 (12.6 %) were swallowed whole, 179 (77.5 %) were partitioned before ingestion, while the handling of 23 (10.0 %) prey was unknown. The largest prey items swallowed whole by the nestlings had a net mass of 100 g. Factors that could affect whether the nestlings swallowed a prey whole were nestling age, net prey mass, and which nestling handled the prey. Candidate models were tested with Akaike's information criterion, and the most parsimonious model of the most supported ones was determined (Table 22). Model 5 was chosen and used for further testing.

Table 22. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting if a prey delivered at the nest was swallowed whole or not by the golden eagle nestlings.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
7	Nestling age + Net prey mass + Nestling ID	4	102.16	0.00	0.64
5	Nestling age + Net prey mass	3	103.39	1.23	0.35
6	Net prey mass + Nestling ID	3	112.45	10.29	0.00
3	Net prey mass	2	112.61	10.45	0.00
4	Nestling age + Nestling ID	3	146.05	43.89	0.00
1	Nestling age	2	146.43	44.27	0.00
2	Nestling ID	2	159.43	57.27	0.00
0		1	160.97	58.81	0.00

The model including nestling age and net prey mass best explained whether the nestlings swallowed a prey whole or partitioned the prey before ingestion (Table 22). The predicted probability of a prey being swallowed whole decreased significantly with increasing nestling age and net prey mass (Table 23).

Table 23. Parameter estimates from the most supported logistic regression model (i.e. model 5 in Table 22). The parameters predict the probability of the golden eagle nestlings swallowing a prey item whole. R^2=0.50.

	Estimate	Std. error	z-value	p	
Intercept	6.116	1.768	3.460	0.0005	***
Nestling age	-0.089	0.030	-2.969	0.0030	**
Net prey mass	-0.041	0.007	-5.740	< 0.0001	***

The nestlings handled 213 birds unassisted. Of these, the nestlings plucked 46 (21.6 %) and did not pluck 119 (55.9 %), while the remaining 48 (22.5 %) could not be scored for plucking. Factors potentially affecting whether the nestlings plucked a bird or not could be nestling age, net prey mass and which nestling were handling the bird. The model with the best fit was identified based on Akaike's information criterion (Table 24). Model 1 was the best fit and was used in further testing.

Table 24. The model selection output of Akaike's information criterion, used to identify the logistic regression model with the factors best predicting if a prey delivered at the nest was plucked or not by the golden eagle nestlings.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
1	Nestling age	2	131.67	0.00	0.46
5	Nestling age + Net prey mass	3	133.04	1.37	0.23
4	Nestling ID	3	133.35	1.68	0.20
7	Nestling age + Net prey mass + Nestling ID	4	134.73	3.06	0.10
3	Net prey mass	2	156.51	24.85	0.00
6	Net prey mass + Nestling ID	3	157.39	25.72	0.00
2	Nestling ID	2	158.65	26.98	0.00
0		1	159.48	27.82	0.00

The nestlings' age was the factor best predicting whether they plucked a bird or not (Table 24). The predicted probability of the nestlings plucking a bird increased significantly with nestling age (Table 25, Figure 11).

Table 25. Parameter estimates from the best fit logistic regression model (i.e. model 1 in Table 24). The parameters predict the probability of nestlings plucking a prey delivered at the golden eagle nest during the breeding season. R^2=0.20.

	Estimate	Std. error	z-value	p	
Intercept	-8.054	1.543	-5.220	< 0.0001	***
Nestling age	0.113	0.024	4.678	< 0.0001	***

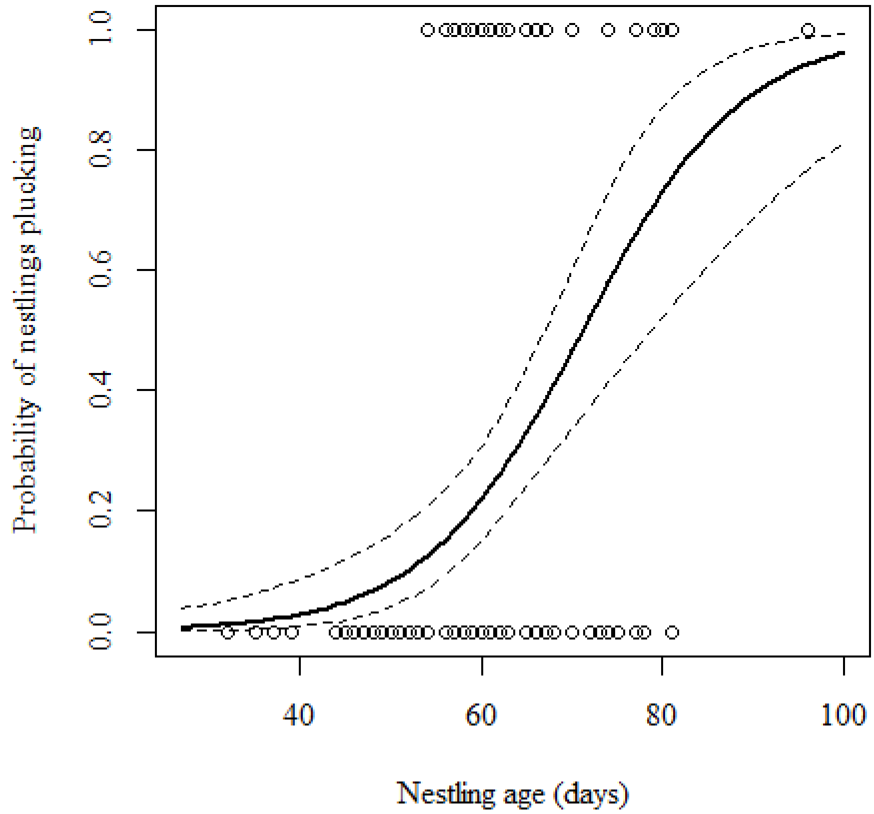


Figure 11. The predicted probability of the golden eagle nestlings plucking a bird delivered at the nest, as estimated by the logistic regression model in Table 25. The solid black line represents the estimated probability, and the dashed lines the upper and lower 95 % confidence intervals. Each circle represents a handled bird and shows whether the nestlings plucked it (1.0) or not (0.0).

The nestlings handled some prey items in several bouts. The number of recorded bouts ranged from 1 to 6. Of the prey handled unassisted, the nestlings ingested 174 (75.5 %) in one bout. The number of bouts increased significantly with net prey mass (Table 26).

Table 26. The parameter estimates of the poisson regression model predicting the number of bouts the nestlings used handling a prey delivered at the golden eagle nest during the breeding season. R^2=0.12.

	Estimate	Std. error	z-value	p	
Intercept	-0.0354	0.0892	-0.397	0.6920	
Net prey mass	0.0022	0.0004	5.336	< 0.0001	***

The nestlings handled 231 prey items unassisted. Of these, both nestlings handled 28 (12.1 %), the smallest nestling monopolised 76 (32.9 %), and the largest monopolised 126 (54.5 %). Which nestling handled the remaining three were unknown. Of the unassisted handling, the largest nestling handled 15 269 g prey mass, and the smallest handled 13 916 g prey mass during the study period. Before the largest nestling fledged, the largest nestling had handled

15 269 g and the smallest 10 619 g. Of the 76 prey items monopolised by the smallest nestling, 17 were delivered after the largest nestling fledged.

Of all monopolised prey items handled until the largest nestling fledged, the mean prey mass handled by the largest nestling were significantly higher than the mean prey mass handled by the smaller nestling (Table 27).

Table 27. The output of a Welsh's t-test predicting the difference in net handled prey mass between the two nestlings during the nestling period of the golden eagle. The analysis did not include prey handled by both nestlings.

			95 % Confidence interval					
	n	Mean	Lower	Upper	t	df	p	
Small nestling	185	35.297	-38.159	-12.113	-3.796	368	0.0002	***
Large nestling	185	60.433						

Discussion

Prey delivered at the nest

The golden eagles delivered 304 prey items at the nest to their two nestlings. The total delivered gross mass was 83 747 g, which resulted in a mean prey mass of 276 g. Earlier studies using video monitoring in Norway at golden eagles' nests, with one nestling, has registered between 71 (Nygård, 2015) and 120 delivered prey items (Dihle, 2015). Günther (2020) video monitored four nests with one to two nestlings and found a mean total delivered gross mass of 66 516 g. When video monitoring a nest with two nestlings, Skouen (2012) registered 181 delivered prey items and a total delivered gross mass of 89 260 g. The mean gross prey mass in previous studies using video monitoring ranges from 484 g to 912 g (Skouen, 2012; Nygård, 2015; Günther, 2020).

When comparing my results to those from earlier studies in Norway using video monitoring, there are some contrasting results. The mean gross prey mass was lower than the one found in earlier studies, and the golden eagles delivered a higher number of prey items in my study than in previous studies (Skouen, 2012; Nygård, 2015; Günther, 2020). Even compared to a nest with two nestlings (Skouen, 2012), my results show a higher number of prey individuals, but there was only a 5.5 kg difference in total gross mass. With two nestlings at the nest, the female may need to resume hunting earlier to fulfil the nestlings' food demand than if there was only one nestling at the nest. Additionally, it may be more advantageous for the parents to deliver small prey, which will result in a lower mean prey mass, like in my study. By delivering smaller prey, the time when the nestlings start to handle prey unassisted could be promoted. Then, the female could be relieved from partitioning prey earlier than if the parents deliver larger prey (Sonerud et al., 2014a).

To my knowledge, the proportion of avian prey in the golden eagles' diet in my study (89 %) is the highest found in studies using video monitoring. Other studies using video monitoring in Norway has found a proportion as low as 34 % avian prey (Dihle, 2015), and others between 65 % and 70 % (Skouen, 2012; Nygård, 2015; Günther, 2020). Johnsen et al. (2007) collected prey remains and pellets in Norway and found a proportion of 73 % avian prey, while Tjernberg (1981) and Nyström et al. (2006) did the same in Sweden and found 66 % and 64 % avian prey in the golden eagles' diet, respectively. Contrarily, Högström & Wiss (1992) found more than 50 % mammals in the golden eagle's diet in Sweden when collecting pellets and remains.

The traditional method of estimating raptor diet has been collecting prey remains and pellets (Tjernberg, 1981; Marquiss et al., 1985), which has been found to underestimate small birds (Redpath et al., 2001; Selås et al., 2007). Additionally, raptors have been found to ingest a larger proportion of smaller prey than larger prey (Slagsvold et al., 2010), which would leave less remains from smaller prey. Large proportions of small birds, like thrushes, may therefore be more common than previous studies, collecting pellets and remains, has found (Tjernberg, 1981; Högström & Wiss, 1992). As in my study, where the golden eagles delivered a large number of thrushes at the nest.

In my study, the golden eagles delivered 58 % thrushes, 15 % ptarmigans, and 5 % mountain hares. In gross mass, there was 36 % mountain hare, 26 % ptarmigan, and 19 % thrush. Previous studies using video monitoring has also found mountain hare, thrushes and ptarmigans to be the most numerous prey in the golden eagles' diet during the breeding season (Skouen, 2012; Nygård, 2015; Günther, 2020). By collecting remains and pellets in Norway, Johnsen et al. (2007) found 51 % ptarmigans in the diet, and Jacobsen et al. (2012) found 64 % mountain hare. To my knowledge, the highest proportion, in numbers, of thrushes in the golden eagle's diet found in earlier studies using video monitoring is 24 % (Skouen, 2012). Tjernberg (1981) and Högström & Wiss (1992), on the other hand, collected pellets and remains and found thrushes to be close to absent in the golden eagle's diet. In gross mass, mountain hares have been the most important prey in previous studies (Jacobsen et al., 2012; Dihle, 2015; Nygård, 2015; Günther, 2020). Ptarmigans have usually accounted for 12 % to 35 % of the gross mass (Jacobsen et al., 2012; Skouen, 2012; Nygård, 2015; Günther, 2020), but it has been found to account for as little as 5 % (Dihle, 2015). In earlier studies using video monitoring the gross mass of thrushes in the diet has been below 5 % (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020). Compared to earlier studies, the amount of ptarmigan and mountain hare are inside the expected interval. The quantity of thrushes is higher than expected by previous studies and contributed largely to the low mean prey mass I found. The proportions of gross mass are close to what has been registered for ptarmigans, somewhat lower for the mountain hare, and higher for thrushes (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020).

The golden eagle has a considerable variation of mammal and bird proportions in its diet (Högström & Wiss, 1992; Johnsen et al., 2007). This large degree of variation reflects the broad diet of the golden eagle, which is regarded as a generalist predator (Watson, 2010). In my study, the large proportion of avian prey mainly consisted of thrushes. The golden eagles delivered a large quantity of thrushes, and small rodents like lemmings and voles were close to absent. Usually, in studies investigating the diet of the golden eagle, there has been a higher quantity of small rodents (Nyström et al., 2006; Skouen, 2012; Dihle, 2015; Günther, 2020). Steenhof & Kochert (1988) found that the quantity of preferred and alternative prey in the golden eagles' diet was associated with the density of preferred prey. This leads me to suggest that thrushes could be an alternative prey to small rodents in years when the availability of small rodents is low. In the study area, game birds are yearly counted along line transects, and at the same time, mammals are registered when observed (Hønsefuglportalen [The game bird portal], 2021). In 2020, the estimate of small rodents was low (Hønsefuglportalen [The game bird portal], 2021), which is in agreement with the low quantity of delivered rodents in 2020. Still, these estimates should be considered with care, as the primary purpose is not to estimate rodent populations.

Prey handling prior to delivery

The golden eagles delivered 20 % of the prey items decapitated. Günther (2020) registered a larger proportion of 33 % decapitated prey. I found that the probability of a delivered prey being decapitated decreased as the nestlings grew older. Günther (2020) found a trend for the same and, in addition, an increased probability of decapitation with gross prey mass. Similarly, Skouen (2012) found that the probability of prey being decapitated or partly eaten decreased with nestling age and increased with gross prey mass. In the Eurasian kestrel (*Falco tinnunculus*), Steen et al. (2010) found the same decreasing probability of decapitation with nestling age. This has also been found in great tits (*Parus major*), with a decreasing degree of prey preparation with nestling age (Barba et al., 1996). The results from earlier studies correspond well with my results (Barba et al., 1996; Steen et al., 2010; Skouen, 2012; Günther, 2020).

The nestlings' gape size limits the swallowing capacity, and young nestlings can only ingest small and soft prey items (cf. Slagsvold & Wiebe, 2007). The skulls of the golden eagles' prey can not be partitioned to fit the nestlings' gape size, and the nestlings may be unable to swallow the head of a delivered prey (cf. Kaspari, 1990). Therefore, early in the breeding season, when the head of a prey item exceeds the nestlings' gape size, it may be removed in advance to reduce the cost of transport to the nest (cf. Sodhi, 1992; cf. Rands et al., 2000). This has been found in merlins (*Falco columbarius*), where the decapitated or plucked prey items had been captured further from the nest (Sodhi, 1992). By removing and possibly ingesting the head, the delivering parent may also reduce the time spent for self-foraging (cf. Rands et al., 2000).

Günther (2020) found a larger proportion of decapitated prey items delivered at the nest. Additionally, he found that increasing gross prey mass increased the probability of decapitation. Thus with a higher mean prey mass, it is expected that the golden eagles deliver a larger proportion of decapitated prey (Günther, 2020). Both my study and those of Skouen (2012) and Günther (2020) showed a decreasing probability of decapitation with nestling age, which is in agreement with the predictions of the feeding constraint hypothesis (cf. Slagsvold & Wiebe, 2007; cf. Steen et al., 2010). As the nestlings grow, their gape sizes increase, and they are able to ingest larger heads (cf. Slagsvold & Wiebe, 2007; cf. Steen et al., 2010). It should be noted, there were some differences in the explanatory variables between my study and those of Skouen (2012) and Günther (2020). Both Günther (2020) and Skouen (2012) found that decapitation increased with gross prey mass. Additionally, adult raptors have been found to leave the head uneaten more often for larger prey (Slagsvold et al., 2010). Both the nestling age and gross prey mass may be noteworthy predictors for the probability of decapitation. Sodhi (1992) found the travel distance to be a predictor for the merlin delivering a prepared prey, either plucked or decapitated. Neither my study nor previous studies video monitoring the golden eagle in Norway have measured the distance between the nest and the capture site, which may be a meaningful predictor together with nestling age and gross prey mass.

Of all avian prey delivered at the nest, 32 % were plucked prior to delivery. Highly corresponding, an earlier study found that 33 % of the birds were plucked before delivery at the nest (Günther, 2020). The probability of a bird being plucked increased with gross mass. Skouen (2012) also found an increased probability of plucked prey with gross prey mass, and Rutz (2003) found that goshawks (*Accipiter gentilis*) plucked larger prey more thoroughly. In my study, the male tended to deliver more plucked prey than the female, which Skouen (2012) did not find.

Plucking may reduce the carrying cost when transporting the prey to the nest from the capture site (cf. Rands et al., 2000). Additionally, Rutz (2003) suggested that plucking increases the prey item's aerodynamic shape, and there should be more to gain in plucking larger prey. As for decapitation, Sodhi (1992) found that the travel distance also increased the probability of plucking before transportation to the nest. Thus, it may be more profitable to pluck larger prey if the distance to the nest is long. In my study, the distance to the capture site is unknown, but it could have an impact. I found a trend for a higher probability of plucked prey delivered by the male. If plucking a prey before transportation reduces the cost, the smaller male may have more to gain in plucking prey, as the relative cost is higher than for the larger female. If the capturing golden eagle decides to ingest some of the prey and thus plucks first, it will also contribute to plucking prior to delivery.

Of the prey delivered at the nest during the study period, 11 % were partly eaten, and 75 % of these were birds. An earlier study found a slightly higher percentage of 19 % partly eaten prey (Günther, 2020). The probability of a delivered prey being partly eaten decreased with nestling age and increased with gross prey mass. In agreement, Skouen (2012) found that the probability of decapitation or partly eaten prey decreased with nestling age and increased with prey mass. In my study, the male tended to be more likely of delivering a partly eaten prey.

I registered a lower proportion of partly eaten prey than Günther (2020) did. This was expected, as the probability of partly eaten prey increased with gross prey mass, and Günther (2020) found a higher mean gross prey mass than I did. The decreasing probability of partly eaten prey with nestling age may be due to the nestlings having a higher food demand or the high proportion of small prey items, which had a lower probability of being partly eaten. By partly ingesting a captured prey, the golden eagles may reduce the carrying cost and reduce the time needed for self-foraging (cf. Rands et al., 2000). By partly eating smaller prey, the gain will be relatively small, and small prey used to self-feed may instead be entirely eaten than transported to the nest. Additionally, the load-size effect predicts that smaller prey should be eaten at the capture site and not transported to the nest (Sonerud, 1992). I found that the probability of both plucking and partly eaten prey tended to be higher if the male rather than the female delivered the prey. The male could be self-feeding to a larger extent than the female, and thus also plucking, because the female was self-feeding at the nest when feeding the nestlings.

Diel delivery pattern

The diel prey delivery pattern of the golden eagles took shape as a bell-shaped curve, with a probability of delivery higher than random between 09:00 and 16:00. Günther (2020) found two peaks rather than one and a probability of delivery higher than random between 08:00 and 19:00. The second peak was from 17:00 until 19:00 (Günther, 2020), which started when the probability of delivery in my study was random. The second peak was also less apparent when only bird deliveries were considered (Günther, 2020). Other studies have found more prey deliveries after midday than before (Dihle, 2015; Nygård, 2015). Compared to previous studies, my results correspond to some extent, but most apparent is the lack of a second peak (Dihle, 2015; Nygård, 2015; Günther, 2020).

Golden eagles are diurnal (Watson, 2010), and with short summer nights in Norway, most of the day during the breeding period can be used for hunting. The lack of an extra peak in the delivery pattern in my study could be due to few mammals in the diet. Günther (2020) included four nests over two years, and a higher number of small rodents were delivered at the nests. In his study, birds were delivered with more even probability throughout the day and mammals with two peaks (Günther, 2020). Günther (2020) explained this difference with birds being diurnal and mammals nocturnal. This appears to be a plausible explanation because when his second peak for delivery of mammals started, the probability for delivery in my study was the same as random. The golden eagles' diel delivery pattern may change between years due to differences in the availability of mammals and birds.

Influence of nestling age

In my study, the number of delivered prey per day increased with nestling age, but fewer prey items were delivered close to fledging. The daily rate of delivered prey items has also been associated with nestling age in the Eurasian kestrel, with a positive U-shaped curve (Steen et al., 2012). Another single-prey loader, the great tit, has also been found to increase the rate of prey deliveries with nestling age (Barba et al., 2009). Blondel et al. (1991) found the blue tit (*Cyanistes caeruleus*) to increase the rate of delivered prey with nestling age and a decrease close to fledging. My results correspond with an expected increase in the delivery rate with nestling age. Still, I found no change in the delivered net prey mass per day. Contrarily, in Steen et al. (2012), the daily rate of prey mass delivered by the Eurasian kestrel was associated with nestling age, with a U-shaped curve. Collopy (1986) studied captive golden eagle nestlings and stated that daily food consumption peaked when the nestlings were between 24 and 44 days old. Thus, my results do not correspond with an expected increase in net delivered mass due to increased food demand.

I found an increase in the number of delivered prey per day, which corresponds with previous studies (cf. Blondel et al., 1991; cf. Barba et al., 2009; cf. Steen et al., 2012). When the nestlings manage to handle prey unassisted, the female is relieved from partitioning prey and may resume hunting (cf. Slagsvold & Sonerud, 2007). The days with the highest numbers of deliveries correspond well with the time the nestlings had started to handle prey unassisted. The last three days before the last nestling fledged, there was no prey delivered at the nest, which may be a way of motivating the nestling to fledge. Additionally, it has been found that the food demand of the nestlings decreases towards fledging (Collopy, 1986). As there was an increase in the delivery rate but no change in delivered net prey mass, it appears that the increase in deliveries of smaller prey items cancelled the increase in delivered prey mass. It is expected that the food demand increases with the nestling age (Collopy, 1986), which was not found in my study. Still, Collopy (1986) based the study primarily on captive nestlings and estimated mass ingested by crop fullness of the wild nestlings, which might be an inaccurate estimate. Additionally, in my study, when the nestlings started handling unassisted, the female did not self-feed from prey delivered at the nest. Therefore, the nestlings ingested a larger proportion of the delivered prey mass. Also, both nestlings in my study successfully fledged, and it appears that the delivered net mass was enough to satisfy the demand of the two nestlings.

During my study period, the male delivered 70 % of the prey items. Former studies using video monitoring in Norway has found the male to deliver between 57 % and 68 % (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020). My results are close to what is found in earlier studies, but the female delivered slightly fewer prey at the nest. The probability of the delivering parent being one or the other did not change as the nestlings grew older. Also, Skouen (2012) found that the delivering parent was not affected by the nestling age. In contrast, Günther (2020) found an increased probability of the delivering parent being the female as the nestlings grew older. Thus, my result corresponds with Skouen (2012) and not Günther (2020).

In golden eagles, the female mainly stays at the nest to feed the nestlings, while the male hunts, especially early in the nestling period (Newton, 1979; Watson, 2010). With two nestlings who started handling prey unassisted quite early, one would expect the female to contribute to hunting to a larger degree, which was not observed. Still, parental investment is a cost, and the female might preserve her energy for later years and not exhaust her energy reserves (cf. Trivers, 1974). The different results compared to Günther (2020) might also be due to the number of nestlings. In my study and in Skouen (2012), there were two nestlings, and at the nests in Günther (2020), the number of nestlings varied between one and two, and were not included as a variable in the models. Possibly, when there are two nestlings, the female contributes to a larger degree early during the nestling period, and thus the change in probabilities might be absent.

The gross prey mass declined with the nestling age, and the golden eagle male was more likely to deliver smaller prey than the female. Additionally, the male had a smaller decrease in gross prey mass than the female as the nestlings grew older. In the Eurasian kestrel, the daily average body mass of single prey items has been found to decrease with nestling age (Steen et al., 2012), and the male has been found more likely of delivering smaller prey than the female (Sonerud et al., 2013). Skouen (2012) found no relationship between the delivering parent and prey mass. Thus, my results do not correspond with previous studies of the golden eagle.

Not all prey delivered at the nest is necessarily captured by the delivering parent, which could be why the male was more likely to deliver smaller prey. The golden eagle male may transfer larger prey to the female, who brings it to the nest, and the male can resume hunting earlier (cf. Sonerud et al., 2013). Therefore, the male may deliver smaller prey than the female but not necessarily capture smaller prey than the female. When the nestlings are young and the female spends most of her time at the nest, the male may more frequently transfer larger prey than delivering it himself. As the nestlings grow older and the female has resumed hunting, the male may instead deliver all the prey he captures himself as the female may be absent at the nest. The decrease in gross prey mass with nestling age might enable the nestlings to handle prey unassisted and thus relieve the female to resume hunting (Sonerud et al., 2014a). Early when the female assisted the nestlings in prey handling, the probability of larger prey was higher. As the nestlings were able to handle prey unassisted, the gross prey mass decreased.

Of the prey delivered at the nest, thrushes were the most common prey type. The probability of a delivered prey being a thrush increased with nestling age, and the probability of a prey item being a thrush increased if the male delivered the item rather than the female. There was an interaction between nestling age and delivering parent. As the nestlings grew older, the female had a larger increase in the probability of delivering a thrush than the male. Nygård (2015) also found that the probability of a prey being a thrush rather than another prey increased with nestling age, and the male delivered a larger proportion of the thrushes than the female. Quite similar, Dihle (2015) found that the probability of a prey being a thrush rather than another bird increased with nestling age. My findings correspond well with earlier studies.

Both Dihle (2015) and Nygård (2015) explained the increased probability of a delivered thrush with an increase in availability, as thrushes hatch later and more fledgelings are available for predation later in the season. Additionally, it is more beneficial to deliver thrushes later as the nestlings will be able to handle a small prey like the thrush unassisted. The male was more likely to deliver a thrush than the female, which fits the ingestion rate hypothesis (cf. Slagsvold & Sonerud, 2007). The ingestion rate hypothesis states that raptor males are smaller than the female to catch small, agile prey during the breeding season (Slagsvold & Sonerud, 2007), including thrushes.

Among the changes in proportions of prey through the nestling period, the most striking was the increase in the proportion of thrushes after the nestlings were 32 days old. This corresponds with the findings of Dihle (2015) and (Nygård, 2015). The proportion of ptarmigans became smaller after the nestlings were 32 days old. Correspondingly, former studies have found a decreased probability of a delivered prey being a ptarmigan rather than other prey as the nestlings grew older (Skouen, 2012; Dihle, 2015; Nygård, 2015). The most noticeable change in prey composition was before and after the nestlings were 32 days old, approximately before and after they started to feed unassisted. The simple presentation of the prey proportions in relation to nestling age seems to be fitting the expected development based on previous studies (Skouen, 2012; Dihle, 2015; Nygård, 2015).

In the first period, mainly the male is hunting and needs to satisfy the energetic demand of both the female and the nestlings. When the female is handling the prey, the size of the prey is not constrained by the nestlings' handling capacity or gape size. Thus, larger prey is more favourable. The decrease in ptarmigans in the diet of the golden eagles has been explained differently. Skouen (2012) explained the decrease with ptarmigans being more vulnerable early in the breeding season (Hannon et al., 2003) and that other prey is more available later. Dihle (2015) stated that ptarmigans were too large for the nestlings to handle unassisted and were therefore not selected as the nestlings grew older. Large prey, like mountain hares and ptarmigans, are likely important to satisfy the energetic need early in the breeding season. In contrast, small prey, like thrushes and small mammals, are important later so the nestlings can handle unassisted and the female may resume hunting (cf. Slagsvold & Sonerud, 2007).

Nestlings feeding unassisted

The first unassisted handling took place at the nest when the nestlings were 27 days old. Earlier studies using video monitoring registered unassisted handling to start when the nestlings were 28 (Dihle, 2015), 44 (Günther, 2020), and 55 days old (Nygård, 2015). Watson (2010) states that unassisted handling would start after the nestling is 35 days old. Thus, the range appears to be broad. The earliest unassisted handling in previous studies using video monitoring in Norway was recorded by Dihle (2015), which were one day later than my observation. The nestlings handled 79 % of the delivered prey items unassisted, which is, to my knowledge, the highest percentage registered using video monitoring in Norway. Earlier studies have found the nestlings to handle between 43 % to 60 % of the prey unassisted (Skouen, 2012; Dihle, 2015; Nygård, 2015; Günther, 2020). When the nestlings were 40 days old, there was a 50 % probability of unassisted handling. Some earlier studies found that this threshold occurred when the nestlings were 47 (Dihle, 2015) and 49 days old (Nygård, 2015). Still, Sonerud et al. (2014a) also found a 50 % probability of unassisted handling when the nestlings were 40 days old, which is corresponding with my own results. I found that the probability of unassisted handling increased with nestling age and decreased with net prey mass. This corresponds with earlier findings in studies using video monitoring in Norway (Skouen, 2012; Sonerud et al., 2014a; Dihle, 2015; Nygård, 2015; Günther, 2020).

The nestlings started handling unassisted earlier than observed in previous studies (Dihle, 2015; Nygård, 2015; Günther, 2020). This leaves more time to handle prey unassisted before fledging, which could explain the high percentage of unassisted handling. Additionally, the mean prey mass in my study was considerably lower than in earlier studies (Skouen, 2012; Sonerud et al., 2014a; Nygård, 2015; Günther, 2020), which may have enabled the nestlings to start handling unassisted earlier and handling a larger proportion of the prey items. Even though small prey items are easier for the nestlings to handle, the results are still surprising with the low proportion of small mammals. Small mammals have a more streamlined shape and smaller appendages than small birds, making them easier to swallow whole when the nestlings are small (cf. Sonerud et al., 2014b). The probability of unassisted handling increased as the nestlings grew older and decreased with increasing net prey mass, which corresponds well with previous studies (Skouen, 2012; Sonerud et al., 2014a; Dihle, 2015; Nygård, 2015; Günther, 2020). As the nestlings grow older, they also get stronger and develop a larger gape size, making them able to handle and swallow more of the prey items. The nestlings handled smaller prey unassisted earlier than larger prey, and for some time, the female still needed to partition larger prey for the nestlings to overcome their gape size constraints (cf. Slagsvold & Wiebe, 2007). Additionally, larger prey could be harder to handle as they have larger bones, stronger ligaments and thicker skull and skin (cf. Slagsvold & Sonerud, 2007), and the nestlings will be limited by their own strength.

Nestlings handling prey

When investigating the nestlings' handling time, I found that net prey mass increased both the net and gross handling time, which was also found in Sonerud et al. (2014a) and Skouen (2012). Additionally, I found that the gross handling time increased if both nestlings handled the prey item rather than monopolising the prey.

In raptors, inter-sibling fights are common, where the larger nestling harass the smaller one (Cramp, 1980). In my study, when both nestlings were registered as handling, they were never handling the prey simultaneously (personal observation). Usually, the largest nestlings would first handle the prey, then leave it, and the small nestling could handle the prey without being harassed (personal observation). As the gross handling time increased if both nestlings handled the prey, it means that they took longer or more frequent pauses in handling when both nestlings handled the prey item. When both nestlings could handle a prey, it may be because there was a temporary surplus of food at the nest, and they were closer to fullness when handling prey, especially the largest nestling. Some earlier studies have estimated handling time for adult golden eagles in captivity (Slagsvold et al., 2010; Grønsdal, 2012), while Skouen (2012) estimated the handling time for both the female and the nestlings at the nest. In her study, other explanatory variables were also included, like nestling age (Skouen, 2012). In my study, nestling age was included in the model selection but was not in the best fit model. Similarly, nestling age was not significant in Skouen (2012) but may have a minor influence.

In my study, the nestlings had a decreasing probability of swallowing a prey whole as they grew older and with an increase in net prey mass. The largest prey swallowed whole by the nestlings had an estimated mass of 100 g. Günther (2020) found the first prey handled unassisted to be swallowed whole, and Skouen (2012) observed small prey items to be swallowed whole by the nestlings.

As the nestlings grew older, they had a lower probability of swallowing a prey whole and thus a higher probability of partitioning it. Early, the nestlings might be too weak to stand for a longer time and tear apart the prey and can only start to partition prey when they are strong enough to stand and tear prey apart (Watson, 2010). Swallowing morsels or a whole prey is limited by the nestlings' gape size (cf. Kaspari, 1990), and larger prey needs to be partitioned before ingested. Therefore, only the smallest prey can be swallowed whole, and some larger ones when the nestlings grow older and their gape size expand. When the nestlings start to handle prey unassisted, they are already used to swallowing morsels partitioned by the female, and the ability to swallow small prey whole might be necessary at the beginning of unassisted handling. As small mammals are easier to swallow whole than avian prey (cf. Sonerud et al., 2014b), other results could be expected with a larger proportion of small mammals delivered at the nest of the golden eagles.

The nestlings in my study had an increased probability of plucking a bird as they grew older. The nestlings were observed to ingest feathers, though it appeared challenging to swallow parts, like wings, of an unplucked bird (personal observation). Skouen (2012) also observed nestlings to swallow feathers but found no increase in the probability of plucking with nestling age but rather a decreased probability of plucking with decreasing prey mass. The non-corresponding results could be due to Skouen (2012) including plucking by both the female and the nestlings in her analysis. In her study, the nestling age appeared non-significant but could have been significant if plucking by the female was excluded from the analysis. My second best fit model included net prey mass, and Skouen (2012) found a decreasing degree of plucking with increasing prey mass. The lack of correspondence between our studies might be due to differences in method or models. As the nestlings started handling unassisted early, it might be demanding to pluck a bird. As they experience the challenges of swallowing the unplucked parts of a bird, they could later start to increase the plucking of birds. Additionally, ingested feathers are probably of a small energetic gain and will be taking up space in the gut.

In my study, the number of bouts increased with net prey mass, which corresponds with Skouen (2012), who found the same. If a prey item exceeds the nestlings' maximum meal size (Collopy, 1986), it should be handled and ingested in several bouts. Additionally, the nestling could also handle in several bouts due to exhaustion as larger prey may be challenging to handle and needs to be handled for a longer time (cf. Slagsvold & Sonerud, 2007).

Out of all prey handled unassisted by the nestlings, the largest nestling handled a larger amount in mass than its smaller sibling. Inter-sibling conflicts are not unusual, where the larger nestling harass or kill the smaller nestling, also when food is abundant (Cramp, 1980). Usually, bill-stabbing can be seen until the nestlings are 20 days old, but if there is a shortage of food, it may continue until late in the nestling period (Watson, 2010). In my study, the largest nestling appeared dominant from early on after hatching until it fledged (personal observation). The results support this observation as the largest nestling handled a larger amount of prey mass. Collopy (1986) found that if the largest nestling is a female, she will dominate the smaller male during the nestling period, and she is earlier capable of consuming more food. When the nestlings are 45-50 days old, the female will be heavier than the male if she is the oldest (Watson, 2010). Still, Newton (1979) state that the female has no advantage at the nest, as the male will develop faster. In my study, the largest nestling became larger than its sibling early and was dominant from an early point in the nestling period (personal observation). Based on earlier observations (Collopy, 1986; Watson, 2010), this leads me to believe that the largest nestling was a female and the smallest a male. The faster development of the male was possibly inhibited because the larger female largely monopolised the prey delivered at the nest. Even though the smallest nestling handled considerably less than the largest one, it still survived and fledged a few days later than the largest.

For future studies

The method for collecting video clips was not ideal for registering handling time and resulted in lapses between the clips. By registering the length of lapses and excluding the handling with lapses influencing the registered handling times, this can be resolved to some extent to reduce the sources of error. Still, future studies should strive to collect continuous video clips if investigating handling, to reduce the sources of error. The method used for registering handling times can be vulnerable for observer drift (Martin & Bateson, 2007), which can be easily resolved by using several observers. Still, when handling times were re-registered, the variation was small. Also, precise definitions are crucial when registering handling times.

Future studies investigating the diet and behaviour during the breeding season of the golden eagle should monitor several dispersed nests over multiple years to reveal potential differences between couples, area, and years. Especially areas where the estimated losses of domestic sheep or reindeer are high should be a focus to determine to what extent the golden eagle includes sheep and reindeer in its breeding diet. By video monitoring the nests, it is possible to study a large variety of ecological factors. Also, this is a one-time effort and are cost- and time-efficient compared to other methods. The study of Sørås et al. (2020) radio-tracked the boreal owl (*Aegolius* funereus) while also video monitoring the nest. Similar methods should also be implemented when studying the golden eagle, and future studies should aim to reveal the distance from the capture sites and the capturing parent while also monitoring the nest to examine the potential influence on prey size and handling prior to delivery at the nest.

Conclusion

By video monitoring a golden eagle's nest during the breeding season, my study shows that thrushes may be an important prey in years with a low abundance of small rodents. Additionally, thrushes have likely been highly underestimated in earlier studies collecting remains and pellets. The golden eagles showed a clear shift between the selection of larger prey early and smaller prey later in the breeding season, likely to ensure that the nestlings could handle prey items unassisted. When food was abundant at the nest, both nestlings handled a single prey, and they took more or longer pauses when handling. Additionally, the largest nestling handled considerably more prey mass than the smaller one through the nestling period. The presence of two nestlings at the nest might also influence the parents' foraging behaviour. With two nestlings, the parents will select more small prey, and the female might contribute to hunting also early in the nestling period to satisfy the nestlings' food demand. Future studies should aim to investigate the breeding behaviour and diet of the golden eagle, both nestlings and adult, using video monitoring and tracking of the adults.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19 (6): 716-723. doi: 10.1109/TAC.1974.1100705.

Artskart [Species maps]. (2021). Trondheim: Artsdatabanken. Available at: https://artskart.artsdatabanken.no/ (accessed: 08.02.2021).

Barba, E., López, J. A. & Gil-Delgado, J. A. (1996). Prey preparation by adult great tits Parus major feeding nestlings. *Ibis*, 138 (3): 532-538. doi: 10.1111/j.1474-919X.1996.tb08074.x.

Barba, E., Atiénzar, F., Marín, M., Monrós, J. S. & Gil-Delgado, J. A. (2009). Patterns of nestling provisioning by a single-prey loader bird, great tit Parus major. *Bird Study*, 56 (2): 187-197. doi: 10.1080/00063650902792049.

Bergo, G. (1990). *Ørneskader på småfe og hjortedyr [Golden eagle damages on sheep and deer]* NINA Forskningsrapport 09/1990. Trondheim: Norwegian Institute for Nature Research (accessed: 17.02.2021).

Blondel, J., Dervieux, A., Maistre, M. & Perret, P. (1991). Feeding ecology and life history variation of the blue tit in mediterranean deciduous and sclerophyllous habitats. *Oecologia* (88): 9-14.

Burnham, K. P. & Anderson, D. R. (2004). Multimodel inference. *Sociological Methods & Research*, 33 (2): 261-304. doi: 10.1177/0049124104268644.

Collopy, M. W. (1983). A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. *The Journal of Wildlife Management*, 47 (2): 360-368. doi: 10.2307/3808508.

Collopy, M. W. (1986). Food consumption and growth energetics of nestling golden eagles. *The Wilson Bulletin*, 98 (3): 445-458. doi: 10.2307/4162270.

Cramp, S. (1980). *The birds of the Western Palearctic: Hawks to bustards*. Handbook of the birds of Europe, the Middle East and North Africa, vol. 2. Oxford: Oxford University Press.

Cramp, S. (1983). *The birds of the Western Palearctic: Waders to gulls*. Handbook of the birds of Europe, the Middle East and North Africa, vol. 3. Oxford: Oxford University Press.

Cramp, S. (1988). *The birds of the Western Palearctic: Tyrant flycatchers to thrushes*. Handbook of the birds of Europe, the Middle East and North Africa, vol. 5. Oxford: Oxford University Press.

Cramp, S. (1993). *The birds of the Western Palearctic: Flycatchers to shrikes*. Handbook of the birds of Europe, the Middle East and North Africa, vol. 7. Oxford: Oxford University Press.

Cramp, S. (1994). *The birds of the Western Palearctic: Crows to finches*. Handbook of the birds of Europe, the Middle East and North Africa, vol. 8. Oxford: Oxford University Press.

Dabao, Z. (2021). *rsq: R-squared and related measures* (Version 2.2). Available at: https://CRAN.R-project.org/package=rsq.

Dahl, E. L., Nilsen, E. B., Brøseth, H. & Tovmo, M. (2015). *Estimering av antall hekkende par kongeørn basert på kjent forekomst i Norge for perioden 2010-2014 [Estimating the number of breeding couples of golden eagles based on known occurrences in Norway during 2010-2014]*. NINA Rapport 1158/2015. Trondheim: Norwegian Institute for Nature Research (accessed: 16.02.2021).

Davies, N. B., Krebs, J. R. & West, S. A. (2012). *An introduction to behavioural ecology*. 4th ed. West Sussex: Wiley-Blackwell.

Davoren, G. K. & Burger, A. E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, 58 (4): 853-863. doi: 10.1006/anbe.1999.1209.

Dihle, I. (2015). *Prey selection and prey handling in two raptors during the breeding season as revealed by the use of video monitoring*. Master thesis. Ås: Norwegian University of Life Sciences.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., et al. (2011). Trophic downgrading of planet earth. *Science*, 333 (6040): 301-306. doi: 10.1126/science.1205106.

Frislid, R. & Jensen, B. (1994). *Norsk pattedyrhåndbok [Norwegian mammalian handbook]*. Oslo: Aschehoug.

Grønnesby, S. & Nygård, T. (2000). Using time-lapse video monitoring to study prey selection by breeding goshawks Accipiter gentilis in central Norway. *Ornis Fennica*, 77: 117-129.

Grønsdal, E. (2012). *Prey handling by a generalist predator, the golden eagle (Aquila chrysaetos)*. Master thesis. Ås: Norwegian University of Life Sciences.

Günther, A. (2020). *Diet, prey deliveries and prey handling of nesting golden eagles (Aquila chrysaetos) in Oppland county, Norway, as revealed by video monitoring of four nests throughout the nestling period*. Master thesis. Ås: Norwegian University of Life Sciences.

Halley, D. J. (1998). Golden and white-tailed eagles in Scotland and Norway. *British Birds*, 91: 171-179.

Halley, D. J. & Gjershaug, J. O. (2008). Inter- and intra-specific dominance relationships and feeding behaviour of golden eagles Aquila chrysaetos and sea eagles Haliaeetus albicilla at carcasses. *Ibis*, 140 (2): 295-301. doi: 10.1111/j.1474-919x.1998.tb04392.x.

Hannon, S. J., Gruys, R. C. & Schieck, J. O. (2003). Differential seasonal mortality of the sexes in willow ptarmigan Lagopos lagopus in northern British Columbia, Canada. *Wildlife Biology*, 9: 317-326. doi: 10.2981/wlb.2003.020.short.

Harrison, J. T., Kochert, M. N., Pauli, B. P. & Heath, J. A. (2019). Using motion-activated trail cameras to study diet and productivity of cliff-nesting golden eagles. *Journal of Raptor Research*, 53 (1): 26. doi: 10.3356/jrr-18-26.

Högström, S. & Wiss, L.-E. (1992). Diet of the golden eagle Aquila chrysaetos (L.) in Gotland, Sweden during the breeding season. *Ornis Fennica*, 69: 6.

Hønsefuglportalen [The game bird portal]. (2021). In *NINA*. Available at: https://honsefugl.nina.no/Innsyn/Innsyn/?regionId=5&rappnivaaId=18 (accessed: 31.03.2021).

Jacobsen, K.-O., Johnsen, T. V., Nygård, T. & Stien, A. (2012). *Kongeørn i Finnmark [The golden eagle in Finnmark]*. NINA Rapport 818/2011. Tromsø: Norwegian Institute for Nature Research. Available at: http://hdl.handle.net/11250/2641076 (accessed: 08.02.2021).

Johnsen, T. V., Systad, G. H., Jacobsen, K.-O., Nygård, T. & Bustnes, J. O. (2007). The occurrence of reindeer calves in the diet of nesting golden eagles in Finnmark, northern Norway. *Ornis Fennica*, 84: 112-118.

Kaspari, M. (1990). Prey preparation and the determinants of handling time. *Animal Behaviour*, 40 (1): 118-126. doi: 10.1016/s0003-3472(05)80671-2.

Katzner, T. E., Kochert, M. N., Steenhof, K., McIntyre, C. L., Craig, E. H. & Miller, T. A. (2020). *Golden eagle (Aquila chrysaetos)*. 2nd ed. Birds of the world: The Cornell Lab of Ornithology. Available at: https://doi.org/10.2173/bow.goleag.02 (accessed: 13.04.2021).

Krebs, C. J. (2014). *Ecology: The experimental analysis of distribution and abundance*. 6th ed. Essex: Pearson Education Limited.

Landskap - NiN [Landscape -NiN]. (2020). Økologiske grunnkart [Ecological base maps]. Trondheim: Artsdatabanken. Available at: https://okologiskegrunnkart.artsdatabanken.no/ (accessed: 08.02.2021).

Lesnoff, M. & Lancelot, R. (2012). *aod: Analysis of overdispersed data*. Available at: http://cran.r-project.org/package=aod.

Lewis, S. B., Fuller, M. R. & Titus, K. (2004). A comparison of 3 methods for assessing raptor diet during the breeding season. *Wildlife Society Bulletin*, 32 (2): 373-385. doi: 10.2193/0091-7648(2004)32[373:acomfa]2.0.co;2.

Marquiss, M., Ratcliffe, D. A. & Roxburgh, R. (1985). The numbers, breeding success and diet of golden eagles in southern Scotland in relation to changes in land use. *Biological Conservation*, 34 (2): 121-140. doi: 10.1016/0006-3207(85)90104-1.

Martin, P. & Bateson, P. (2007). *Measuring behaviour*. 3rd ed.: Cambridge University Press.

Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. Available at: https://cran.r-project.org/package=AICcmodavg.

Miljødirektoratet. (2020a). *Erstattet sau og lam etter tapsårsak [Compensated sheep and lambs by loss cause]*. www.miljodirektoratet.no: Miljødirektoratet.

Miljødirektoratet. (2020b). Erstatning for rein [Compensation for reindeer]. In *Miljødirektoratet*. Available at: https://rovbase.no/erstatning/rein.

Moss, E. H. R., Hipkiss, T., Oskarsson, I., Häger, A. & Eriksson, T. (2012). Long-term study of reproductive performance in golden eagles in relation to food supply in boreal Sweden. *Journal of Raptor Research*, 46 (3): 248-257. doi: 10.3356/jrr-11-48.1.short.

Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78 (3): 691-692. doi: 10.2307/2337038.

Newton, I. (1979). *Population ecology of raptors*. Berkhamsted: T & A D Poyser Ltd.

Nygård, M. (2015). *Diet and prey handling at a nest of the golden eagle (Aquila chrysaetos) in Oppland County, Norway*. Master thesis. Ås: Norwegian University of Life Sciences.

Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P. & Dalén, L. (2006). Golden Eagles on the Swedish mountain tundra - diet and breeding success in relation to prey fluctuations. *Ornis Fennica*, 83 (4): 145-152.

R Core Team. (2020). *R: A language and environment for statistical computing.* (Version 4.0.3). Vienna, Austria: R Foundation for statistical computing. Available at: https://www.R-project.org/.

Rands, S. A., Houston, A. I. & Gasson, C. E. (2000). Prey processing in central place foragers. *Journal of Theoretical Biology*, 202 (2): 161-174. doi: 10.1006/jtbi.1999.1048.

Redpath, S. M., Clarke, R., Madders, M. & Thirgood, S. J. (2001). Assessing raptor diet: comparing pellets, prey remains, and observational data at hen harrier nests. *The Condor*, 103: 184-188. doi: 10.1093/condor/103.1.184.

Rutz, C. (2003). Assessing the breeding season diet of goshawks Accipiter gentilis: biases of plucking analysis quantified by means of continuous radio-monitoring. *Journal of Zoology*, 259 (2): 209-217. doi: 10.1017/s0952836902003175.

Selås, V., Tveiten, R. & Aanonsen, O. M. (2007). Diet of common buzzards (Buteo buteo) in southern Norway determined from prey remains and video recordings. *Ornis Fennica*, 84: 97-104.

Simmons, R. E., Avery, D. M. & Avery, G. (1991). Biases in diets determined from pellets and remains: Correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research*, 25 (3): 63-67.

Skouen, S. K. (2012). *Assessing diet and prey handling in golden eagles (Aquila chrysaetos) by video monitoring at nest*. Master thesis: Norwegian University of Life Sciences.

Slagsvold, T. & Sonerud, G. A. (2007). Prey size and ingestion rate in raptors: importance for sex roles and reversed sexual size dimorphism. *Journal of Avian Biology*, 38 (6): 650-661. doi: 10.1111/j.2007.0908-8857.04022.x.

Slagsvold, T. & Wiebe, K. L. (2007). Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. *Animal Behaviour*, 73 (4): 691-700. doi: 10.1016/j.anbehav.2006.05.021.

Slagsvold, T., Sonerud, G. A., Grønlien, H. E. & Stige, L. C. (2010). Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology*, 41 (4): 488-497. doi: 10.1111/j.1600-048X.2010.05081.x.

Sodhi, N. S. (1992). Central place foraging and prey preparation by a specialist predator, the merlin. *Journal of Field Ornithology*, 63 (1): 71-76. doi: 10.2307/4513664.

Soetaert, K. (2019). *plot3D: Plotting multi-dimensional data*. Available at: https://CRAN.R-project.org/package=plot3D.

Sonerud, G. A. (1992). Functional responses of birds of prey: biases due to the load-size effect in central place foragers. *Oikos*, 63 (2): 223-232. doi: 10.2307/3545382.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2013). Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. *Oecologia*, 172 (1): 93-107. doi: 10.1007/s00442-012-2491-9.

Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G.-H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., et al. (2014a). Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology*, 25 (4): 762-772. doi: 10.1093/beheco/aru053.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014b). Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. *Animal Behaviour*, 96: 31-38. doi: 10.1016/j.anbehav.2014.07.011.

Steen, R. (2009). A portable digital video surveillance system to monitor prey deliveries at raptor nests. *Journal of Raptor Research*, 43 (1): 69-74.

Steen, R. (2010). *Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (Falco tinnunculus)*. Doctoral thesis. Ås: Norwegian University of Life Sciences.

Steen, R., Løw, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. (2010). The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. *Animal Behaviour*, 80 (1): 147-153. doi: 10.1016/j.anbehav.2010.04.015.

Steen, R., Sonerud, G. A. & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (Falco tinnunculus). *Journal of Ornithology*, 153 (4): 1087-1099. doi: 10.1007/s10336-012-0838-y.

Steenhof, K. & Kochert, M. N. (1988). Dietary responses of three raptor species to changing prey densities in a natural environment. *The Journal of Animal Ecology*, 57 (1): 37. doi: 10.2307/4761.

Stien, A., Hansen, I., Langeland, K. & Tveraa, T. (2016). *Kongeørn som tapsårsak for sau og lam 2014-2015 [The golden eagle as the cause of lost sheep and lamb 2014-2015]*. NINA Rapport 1285/2016. Tromsø: Norwegian Institute for Nature Research. Available at: http://hdl.handle.net/11250/2402971 (accessed: 08.02.2021).

Strann, K.-B., Frivoll, V. & Sortland, F. (2013). *Overvåking av beitende sau og lam på utmarksbeite i Himmeltindmassivet, Vestvågøy kommune i 2013 [Surveillance of grazing sheep and lambs at rangeland in Himmeltindmassivet, Vestvågøy municipality in 2013]*. NINA Rapport 990/2013. Tromsø: Norwegian Institute for Nature Reseach. Available at: http://hdl.handle.net/11250/2643111 (accessed: 08.02.2021).

Sulkava, S., Huhtala, K., Rajala, P. & Tornberg, R. (1998). Changes in the diet of the golden eagle Aquila chrysaetos and small game populations in Finland in 1957-96. *Ornis Fennica*, 76: 1-16.

Sørås, R., Gundersen, O. A., Steen, R. & Sonerud, G. A. (2020). Returning for more prey? Foraging in provisioning male boreal owls (Aegolius funereus). *Journal of Ornithology*, 161 (1): 171-181. doi: 10.1007/s10336-019-01710-6.

Tjernberg, M. (1981). Diet of the golden eagle Aquila chrysaetos during the breeding season in Sweden. *Ecography*, 4 (1): 12-19. doi: 10.1111/j.1600-0587.1981.tb00975.x.

Tornberg, R. & Reif, V. (2007). Assessing the diet of birds of prey: a comparison of prey items found in nests and images. *Ornis Fennica*, 84: 21-31.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14 (1): 249-264. doi: 10.1093/icb/14.1.249.

Warren, J. T., Mysterud, I. & Lynnebakken, T. (2001). Mortality of lambs in free-ranging domestic sheep (Ovis aries) in northern Norway. *Journal of Zoology*, 254 (2): 195-202. doi: 10.1017/s095283690100070x.

Watson, J. (2010). *The golden eagle*. 2nd ed.: T&AD Poyser.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*: Springer-Verlag New York. Available at: https://ggplot2.tidyverse.org.

Wickham, H., Averick, M., Bryan, J., Chang, W., D'Agostino McGowan, L., François, R., Grolemund, G., Hayes, A., Lionel, H., Hester, J., et al. (2019). Welcome to tidyverse. *Journal of Open Source Software*, 4 (43).

Ydenberg, R. C. (2007). Provisioning. In Stephens, D. W., Brown, J. S. & Ydenberg, R. C. (eds) *Foraging: behavior and ecology*, p. 32. Chicago: University of Chicago Press (accessed: 20.10.2020).

Appendix A

The model selection output of Akaike's information criterion, used to identify the logistic regression model best predicting the golden eagles' diel delivery pattern. Data were collected at a golden eagle nest during the breeding season in 2020.

Model	Explanatory variables	K	AIC	ΔAIC	AIC-weight
1	I(cos(2*pi*Hour/24)) + I(sin(2*pi*Hour/24))	3	1045.13	0.00	0.50
2	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))	5	1046.35	1.22	0.27
3	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))	7	1049.00	3.87	0.07
5	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))	11	1049.06	3.93	0.07
4	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))	9	1049.29	4.16	0.06
6	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)) + I(cos(6*2*pi*Hour/24)) + I(sin(6*2*pi*Hour/24))	13	1051.53	6.40	0.02
0		1	1167.23	122.10	0.00

Appendix B

The parameter estimates from the linear regression model predicting the length of the golden eagle nestlings' gross handling time of prey at the nest during the breeding season.

	Estimate	Std. error	t-value	p	
Intercept	0.263	0.183	1.442	0.151	
Category handling 2	-0.090	0.125	-0.724	0.470	
Category handling 3	0.291	0.084	3.450	0.0007	***
Category handling 4	0.514	0.103	4.978	< 0.0001	***
Net prey mass	0.992	0.010	9.968	< 0.0001	***

The parameter estimates from the linear regression model predicting the length of the golden eagle nestlings' net handling time prey at the nest during the breeding season.

	Estimate	Std. error	t-value	p	
Intercept	0.213	0.224	0.955	0.341	
Category handling 2	-0.232	0.164	-1.414	0.160	
Category handling 3	0.263	0.099	2.648	0.009	**
Category handling 4	0.460	0.203	2.261	0.026	*
Net prey mass	1.012	0.123	8.227	< 0.0001	***

Appendix C

The models with potential explanatory variables tested with AIC, using data from a golden eagle's nest video monitored in 2020. All models were tested as a generalised linear model.

Response variable	Explanatory variables	Distribution
Decapitated prey	Nestling age + Gross prey mass + Delivering parent + Nestling age * Gross prey mass + Gross prey mass * Delivering parent	Binomial
Plucked bird	Nestling age + Gross prey mass + Delivering parent + Nestling age * Gross prey mass + Gross prey mass * Delivering parent	Binomial
Partly eaten prey	Nestling age + Gross prey mass + Delivering parent + Nestling age * Gross prey mass + Gross prey mass * Delivering parent	Binomial
Gross prey mass	Nestling age + Delivering parent + Nestling age * Delivering parent	Normal
Delivered prey thrush or other	Nestling age + Delivering parent + Nestling age * Delivering parent	Binomial
Unassisted handling or not	Nestling age + Gross prey mass + Net prey mass + Nestling age * Gross prey mass + Nestling age * Net prey mass	Binomial
Gross handling time	Nestling age + Net prey mass + Nestling ID	Normal
Net handling time	Nestling age + Net prey mass + Nestling ID	Normal
Prey swallowed whole	Nestling age + Net prey mass + Nestling ID	Binomial
Nestlings plucking	Nestling age + Net prey mass + Nestling ID	Binomial

Appendix D

The generalised linear models tested to examine the effect of nestling age on the response variables, using data from a golden eagle's nest video monitored in 2020.

Response variable	Explanatory variable	Distribution
Number of prey delivered per day	Nestling age	Poisson
Prey mass delivered per day	Nestling age	Normal
Delivering parent	Nestling age	Binomial
Number of bouts	Nestling age	Poisson

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