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# **Diet, diel activity pattern and prey handling of nesting hawk owls (*Surnia ulula*) as revealed by video monitoring**

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## Abstract

I used video monitoring to record prey deliveries at four nests of the northern hawk owl (*Surnia ulula*) in southern Norway. One nest was monitored in May 2014, while the three other nests were monitored in May-July 2017. Brood size varied from four to eight and no nestlings died during the monitoring. During the net total video monitoring of 960 hours, a total of 680 prey items were recorded delivered at the nest, giving a total gross prey body mass of 23016.8 g. Microtines (*Arvicolinae*) were the most common prey by number and gross prey body mass, making up 92.8% and 94.5%, respectively of identified prey. Of the microtines, *Microtus* voles were the most common prey by number and by gross prey body mass. In total 53 prey items were identified as Norway lemming (*Lemmus lemmus*) and 26 were identified as avian prey. The probability of a prey delivered at the nest being a Norway lemming increased throughout the season, while the probability of an avian prey tended to increase throughout the season. The probability that a prey item was delivered by the female rather than the male increased with nestling age, and was  $> 0.5$  when the oldest nestling in a brood was 15 days old or more. The hawk owl delivered prey at all hours, but the probability of a prey delivery had two marked peaks, one after sunrise and one before sunset, and was low around midnight. There was an increase in number of prey items delivered per nestling per day with increasing nestling age, and the number of prey delivered at the nest per day increased with number of nestlings in the nest. The probability of a prey being decapitated prior to delivery increased with prey body mass. The probability of a nestling feeding unassisted rather than being fed by the female did not exceed 0.50 during the nestling period, and was predicted to exceed 0.50 when the fledglings were 43 days old. Handling time when the female fed the nestlings, tended to decrease with nestling age, probably because the size of the pieces of a prey that the female fed to the young increased with the nestling age.

## Sammendrag

Jeg brukte videoovervåking til å filme byttedyrleveranser ved fire reir av haukugle (*Surnia ulula*) i Sør-Norge. Ett reir ble overvåket i mai 2014, mens de tre andre reirene ble overvåket i mai-juli 2017. Kullstørrelsen varierte fra fire til åtte og ingen av ungene døde under overvåkingen. I løpet av netto total video overvåking på 960 timer, ble totalt 680 byttedyr registrert levert på reir, noe som ga en total brutto byttedyrkroppsmasse på 23016,8 g. smågnagere var de vanligste byttedyrene etter nummer og brutto byttedyrkroppsmasse, og utgjorde 92.8% og 94.5%, henholdsvis av identifiserte byttedyr. Av smågnagerne var *Microtus* det vanligste byttedyret etter nummer og brutto byttedyrkroppsmasse. Totalt 53 byttedyr ble identifisert som Lemen (*Lemmus lemmus*) og 26 ble identifisert som fugl. Sannsynligheten for at et lemen ble levert på reiret økt gjennom sesongen, mens sannsynligheten for fugl tenderte til å øke gjennom sesongen. Sannsynligheten for at et byttedyr ble levert av hunnen heller enn hannen, økte med alderen på ungene, og ble  $> 0.5$  da den eldste ungene i reiret var 15 dager gammel eller mer. Hauk ugle levert byttedyr hele døgnet, men sannsynligheten for byttedyr levering hadde to markerte topper, en etter soloppgang og en før solnedgang, mens var lavere rundt midnatt. Det var en økning i antall byttedyr levert per unge per dag med økende alder på ungene, og antall byttedyr levert på reiret per dag økte med antall unger i reiret. Sannsynligheten for at et byttedyr ble levert uten hode, økte med byttedyrkroppsmassen. Sannsynligheten for at en unge spiste selv heller enn å bli matet av hunnen, oversteg ikke 0.50 i løpet av reir perioden, og var predikert til å overskride 0.50 da ungene var 43 dager gammel. Håndteringstiden når hunnen matet ungene tenderte til å reduseres med alderen på ungene, sannsynligvis fordi størrelsen på bitene av et byttedyr som hunnen matet til ungene økte med alderen på ungene.

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## Introduction

In all organism morphology, physiology, life history and behavior are optimized to be best adapted to the environmental condition they live in to maximize fitness. What is optimal will be a trade-off between benefit and cost. According to the optimal foraging theory a predator should hunt the prey yielding the highest net gain of energy per handling time, with a consideration of constraints like predation risk (Schoener 1971). Different prey are ranked by their profitability which affects the decisions a predator takes (Pyke 1984). Handling time is defined as the total time spent capturing, preparing and ingesting a prey (Kaspari 1990). In birds, preparation time is a varying component of handling time (Kaspari 1990; Sonerud et al. 2014). Raptors catches prey with their feet and use their specialized bill to partition a prey into pieces that can be ingested (Slagsvold & Sonerud 2007). Because of these morphological adaptations, raptors may take prey that their nestlings cannot handle, and their need of assistance decreases with age, increases with prey body mass, and is higher for avian prey than for mammalian prey of same mass (Sonerud et al. 2014). Limitation in swallowing capacity is consider as a constraint in their choice of prey (Slagsvold & Sonerud 2007). Provisioning for nestlings is defined as collecting and preparing prey into suitable size for ingestion and the work is divided between the parents, and it is a trade-off between benefits for nestlings and cost for parents for lost time for self-foraging (Sonerud et al. 2014). Asymmetric parental roles where the female does incubation, brooding and feeding of nestlings, while the male providing food and later assisted by the female, if at all are unique among raptors (Sonerud et al. 2014).

Asymmetrical parental roles are related to sexual size dimorphism (RSD), where females are larger than males (Sonerud et al. 2014). This differential selection is related to diet and increases from insects via reptiles and mammals to birds and with relative prey size (Sonerud et al. 2014). Asymmetric roles, is an adaption to the conflict between time spent collecting and preparing food to nestlings, and it is an optimization of spending the time efficiently in provisioning dependent nestlings (Sonerud et al. 2014).

This is also the case for the northern hawk owl (*Surnia ulula*) hereafter termed hawk owl. Males hunt mostly mammals that are about 12 % of their body mass (Mikkola 1972; Kertell 1986).

Compared to other owl species that occur in Norway, few studies have been done on hawk owl in the world. Like the great grey owl (*strix nebulosa*), the hawk owl lives a nomadic life and is a specialist on microtines (*Arvicolinae*) (Cramp 1985; Sonerud 1997). Hawk owls in Norway are part of the Fennoscandia population (Saurola 2006). It is well known that the density of microtine in boreal and arctic parts of Fennoscandia fluctuate cyclically with peaks 3-4 years (Hagen 1952; Sonerud 1988). These fluctuations are at different cyclic stages through Fennoscandia (Myrberget 1973). As a response of this variation in food availability, hawk owl has adapted to invade and breed temporarily in areas with high abundance of prey (Mikkola 1972; Sonerud 1994). This numerical response can be reinforced by previous egg laying and larger clutches (3-13) (Hörnfeldt 1991).

Hawk owls are diurnal, which is beneficial at northern latitudes where it is almost continuous daylight during the breeding season (Cramp 1985). Hawk owls locate their prey visually from elevated perches like on topmost branch of a tree, and during the search they are using a pause-travel tactic in search of food (Sonerud 1992b). Baekken et al. (1987) estimated home range size of three nesting hawk owl males to be 140 ha, 217 ha and 390 ha. Breeding density is little studied, in Norway there have been found six pairs in 50 km<sup>2</sup> (Sonerud 1997). In fact, it seems to be tolerant to other raptors even in the territory, in spite of its aggressive behaviour to e.g. people close to the nest (Mikkola 1976).

The breeding habitat of hawk owls is typical open or moderately dense coniferous or mountain birch forest, and it is tightly linked to the hunting habitat (Duncan & Harris 1997). Preferred habitat changes with season and the most crucial factor is snow cover (Sonerud 1986; Sonerud 1997). According to optimal foraging theory, searching should be done in habitats yielding the highest net gain of energy (Sonerud 1986). When the snow covers the ground microtines are less available. But unlike *Microtus* voles (field vole (*Microtus agrestis*) and root vole (*Microtus oeconomus*)), bank voles (*Myodes glareolus*) forage on upper parts of young trees above snow (Hansson & Zejda 1977; Montgomery 1980), and therefore be more exposed to the hawk owl. Sonerud (1986) and Nybo & Sonerud (1990) found that bank voles were primary in forests, while *Microtus* voles were in clear-cuts, and that the diet of hawk owls in early spring when snow covered the ground had a high proportion of bank voles, while when the snow started to melt, the availability of the preferred *Microtus* voles species (on average heavier than bank voles, but with and equal handling time) increased, and the diet consisted mostly of *Microtus* voles. This switch in diet was suggested to be a switch in

hunting habitat from forest to clear-cuts as the snow melting, and the prey availability was greatest just after snow melt and decreased as the vegetation leafs out in the clear-cuts (Sonerud 1986; Nybo & Sonerud 1990; Jacobsen & Sonerud 1993).

Sonerud (1986) found that among non-nesting hawk owls, Eurasian kestrels (*Falco tinnunculus*) and common buzzards (*Buteo buteo*), the hawk owl was the most effective hunter. Due to its high strike success, it captured 1.04 prey per hour when the ground was snow free, nearly twice as much as the Eurasian kestrel and the common buzzard did. When the ground was snow covered however, the hawk owl had an even higher strike success (0.75), but number of strikes per hour had dropped, so it caught only 0.24 prey per hour hunting.

Another behaviour adaption known by hawk owl is food caching (Kertell 1986; Sonerud et al. 1987; Gniadek & Holt 2017). In the breeding season, they cache food nearby the nest and can feed nestlings continuously (Huhtala et al. 1987). Caching behaviour by hawk owl is also known during the winter (Schaefer et al. 2007).

During the breeding season, the hawk owl male is a single-prey loaded central place forager. The energy spent during a hunt includes search, capture and preparation and transport of prey (Sodhi 1992). The cost of transporting prey from capture site to nest is related to distance traveling and prey size (Schoener 1971). The profitability of a prey will be different between self-foraging and foraging to feed mate or nestling due to the load-size effect, by that small prey are more likely to be consumed at the capture site than larger prey and its positive correlated with distance to the nest (Sonerud 1992a). Thus, during the breeding season there is a difference between total prey composition and prey delivered at the nest i.e. underestimation of small prey (Sonerud 1992a). In the Eurasian kestrel, the male selectively allocated small prey directly to nestlings and larger prey to the female outside the nest (Sonerud et al. 2013). This will give a false size bias in prey selection between male and female if only the nest is video monitored.

During the first two weeks of the nestling period, the provisioning hawk owl male deliver most of the prey at the nest to further provisioning by the female, whereas after two weeks, prey items are usually given to the female outside the nest (Huhtala et al. 1987). The male with prey will usually vocalize in the vicinity of the nest, and the female will then come and



take the prey from the male and fly to the nest for feeding the young or she will cache it (Kertell 1986; Huhtala et al. 1987; Sonerud et al. 1987).

The diel activity pattern of hawk owls has been studied at three nests based on recording nest visits with an automatic recorder (Huhtala et al. 1987). Our knowledge of the hawk owl's prey composition during the breeding season has been based on collecting pellets and prey remains, and on field observations (e.g.(Hagen 1952; Mikkola 1972; Brennan & Lauff 1998; Gniadek & Holt 2017). Studies on other raptors suggest that pellets and prey remains, underestimate the total amount of prey and gives a skewed estimate regarding to prey of different sizes and types (Tornberg & Reif 2007; Slagsvold et al. 2010). In the last few years, video monitoring has been successfully used to identify of prey delivered to the nest of several raptors (Smithers et al. 2005; Glass & Watts 2009; Steen 2009). This method would give a more precise estimate and provide valuable information about the behaviour of the study species (Selas et al. 2007; Sonerud et al. 2014). The purpose of my study on nesting hawk owls by use of video monitoring were to find out; 1) How is the prey composition? 2) Is it a change in number of prey deliveries at the nest with number and age of nestlings? 3) How is the diel activity pattern? 4) Who is delivery parent, and does it change? 5) What affecting decapitation prior to delivery? 6) When do nestlings feed more unassisted? 7) What affecting handling time? To the best of my knowledge, this is the first study on nesting hawk owl done by video monitoring. A better understanding of the hawk owl is the key to strength the management and conservation strategies for the hawk owl and its prey.

## Methods

### Study area and video monitoring

This study was conducted in Øyer and Lillehammer municipalities in Oppland County in southern Norway 61° 11' 59 N; 10° 33' 1 E. There were in total video monitored four nests of hawk owl (hereafter referred to as nest 1, nest 2, nest 3 and nest 4). Three of the nests were video monitored in 2017 (nest 1, nest 2 and nest 3) and the fieldwork was done by me. Nest 4 was video monitored in 2014 by Helge Grønlien. The nests were in two different areas, nest 1 and nest 2 were close up to the treeline, while nest 3 and nest 4 were in coniferous forest further down. The treeline in the area has been estimated to be at an altitude of 1100 (Rekdal 2017). The average distance to nearest neighbour nest was 3.1 km (range 1.6-4.5 km), and the distance between the two nests furthest away from each other was 11 km (nest 2 and nest 4). Two nest were video monitored from middle of May (nest 1 and nest 4) and the last two (nest 2 and nest 3) from middle of June (table 1). The number of hours with daylight was 17.27 hours (04:20-22:10) on 13 May and number of hours with daylight was 19.32 hours (03:40-22:59) on 23 June (TimeandDateAS 2018). The net total video monitoring were 960 hours and 8 minutes.

To estimate age of nestlings, I used back-dating from the day the nestlings left the nest as recorded on the video. Huhtala et al. (1987) found that the mean age when a nestling left the nest was 23 days, and that the interval between nestlings leaving the nest was c. two days. The end of the video monitoring in a nest was the day when all the nestlings had left the nest, with two exceptions (see below). Because of large brood sizes and inter-brood age differences, I used the age of oldest nestling still in the nest as variable of nestling age in statistical tests. All 25 hawk owl nestlings in this study survived the nestling period.

The abundance of microtines in my study area, is based a trapping site which annually has conducted trapping since 1981. The site is located 40 km south of my study area in a coniferous forest, with an altitude of c. 600 m. Trapping results in 2017 indicated high density of microtine and it was estimated to be a rise year with a possible peak in 2018. Results from trapping data conducted in 2014 also indicated high density of microtines and this year was estimated to be a top year. Because of the distance to my study area is not too far, is it

therefore likely that microtines were abundant also in my study area this two years (G. A. Sonerud, pers. comm.).

Nest 1 was video monitored in 2017 in Øyer. There were altogether seven nestlings, one probably fledged on 21 May, two fledged on 24 May and it were four left when the recording stopped on 24 May. There was a stop in recording between 17-23 May. The nest was in a nest-box with a circular entrance hole and it was in a birch (*Betula* ssp.), at edge of an open forest dominated by birch close to the treeline. The altitude was 930 and the area around was dominated by bog with mountain vegetation southeast and some dairy farms close by. During the video monitoring, snow covered most of the vegetation. The airline distance to nearest neighbour nest was 1.6 km (nest 2).

Nest 2 was video monitored also in 2017 in Øyer. There were six nestlings, one fledged on 27 June, four probably fledged between 28 June and 1 July and the last nestling fledged on 2 July. There was a stop in recording between 25-26 June and 28 June -1 July. The nest was in a nest-box with an open front put up in a Norwegian spruce (*Picea abies*). It was in a forest patch dominated by spruce close to the treeline. The altitude was 940 and the area around was dominated by bogs with mountain vegetation northeast and some dairy farms close by. During video monitoring snow did not cover the vegetation. The airline distance to nearest neighbour nest was 1.6 km (nest 1).

Nest 3 was video monitored in 2017 in Lillehammer. There were four nestlings, one fledged on 5 July, one fledged on 8 July and last two nestling fledged on 9 July. The nest was in a nest-box with a large rectangular entrance hole in front put up in a pine (*Pinus sylvestris*). The area around was dominated by bogs and coniferous forest with clear-cuts, and the altitude was 686. The airline distance to nearest neighbour nest was 4.5 km (nest 4). The late hatching and the small brood size suggest this was likely a pair with second breeding attempt, probably because of breeding failure due to predation earlier in the season.

Nest 4 was video monitored in 2014 in Lillehammer. There were eight nestlings, two fledged between 19 and 20 May, one fledged on 23 May, one fledged on 24 May, one fledged on 26 May, two fledged on 28 May and one was still in the nest when the recording ended on 30 May. The nest was in a nest-box with a circular entrance hole put up in a Norwegian spruce tree. It was located in a forest patch dominated by Norwegian spruce. The altitude was 720

and the area around was dominated by bogs and coniferous forest with clear-cuts. The airline distance to nearest neighbour nest was 4.5 km (nest 3).

**Table 1.** *Summary of the video monitoring of four hawk owl nests in Oppland county, southern Norway. Recording time is the time when the video monitoring system was operational. Brood size is based on number of nestlings at the start of the recording. Nestling age is based on the oldest nestling at the start of recording. \*=Systematic error, due to recording problems (see below).*

<b>Nest ID</b>	<b>Recording period</b>	<b>Recording time</b>	<b>Brood size</b>	<b>Nestling age (d)</b>
Nest 1	13-24 May 2017	120 hours and 58 minutes	7	15
Nest 2	22 June - 2 July 2017	149 hours and 14 minutes	6	18
Nest 3	23 June - 9 July 2017	398 hours and 31 minutes*	4	11
Nest 4	16-30 May 2014	291 hours and 25 minutes	8	20

## **Video monitoring**

To monitor prey deliveries by the hawk owl, a portable video surveillance system was used, as described by Steen (2009). The system consisted of a camera equipped with a wide-angle lens, connected via a cable to a mini digital video recorder (mini DVR) which was placed in a plastic container on the ground. The recordings were saved on a SD card. The mini DVR contained a video motion detection sensor. The sensitivity and detection area to trigger a recording were adjusted for each nest to be sure that all prey deliveries were recorded. Resolution was set to 704 x 560 pixels and a frame rate of 25 pictures per s. A 12V-battery (80Ah) was used to provide power to the camera and the mini DVR. Nest 3, which was farthest away from a road (1.2 km), was equipped with a solar cell that charged the battery. At the other three nests, I replaced the battery when changing the SD card (every 3-4 days).

Two different mini DVRs were used. At nest 2 and nest 3, a mini DVR which supported a SD card up to 32 gigabytes was used. It recorded 5 s before each movement that triggered the sensor and 10 s afterwards, i.e. 15 s for each video clip. At nest 1 and nest 4, a mini DVR which only supported a SD card up to 2 gigabytes was used. It started recording when the sensor was triggered, so recording time was 10 s for each video clip.

The most important limit of the system was the SD card. The number of days it could record until it became full, depended on several factors, e.g. sensitivity level, where the motion

detection area was placed, nest-box type (in an open nest box there was more influence from the environment), Brood size and nestling age.

Because the nest boxes had different shapes, the camera was placed and angled differently at each nest box. For nest 2, which was in an open nest box, the camera was placed in the upper right back corner, pointing towards the entrance. The other three nests were in nest-boxes with removable lid, and this lid was replaced by a custom-made lid with a camera inside. The camera then recorded from above, and in the best possible way pointing towards the entrance. For the two smallest boxes (nest 1 and nest 4) it was difficult to position the camera in such way to be able to identify prey to species.

During the processing of the data I discovered an error in the video system at nest 3 by that the sensor did not reliably trigger by movement to do recording. This was mainly apparent when the camera was in night mode, i.e. black and white, between 22 p.m. and 7 a.m.). It is therefore likely that not all prey have been recorded at this nest. Sometimes the camera was suddenly triggered and started recording after the female had started feeding the young. Thus, I had to estimate time of prey delivery in 18 cases, based on video clips made before the delivery and the video clip with the prey. In daytime recordings, I could not find any recording where the female had left or entered the nest that has not been recorded, but sometimes there was long time between recordings compared with the other nests. Sometimes that the recorder did not stop recording and continued until the maximum duration for a single recording (17 min). These long video clips turned out to provide valuable information about prey handling. The data from this nest are thus not reliable when it comes to the rate of prey deliveries, but provided exact data on prey handling and handling time. This systematic error is considered in the analysis of the data.

### **Identifying prey from video monitoring**

After the fieldwork had been completed, I looked through all the video clips and registered times when the parents entered the nest-box, left the nest-box, and delivered a prey. Then, together with Geir A. Sonerud, I watched all the recordings with deliveries of prey, using VLC media player in slow motion or frame by frame on a TV screen in search of the best frame to identify prey. Every prey delivered at the nest was identified to the lowest taxonomic level possible. Prey were identified from body characteristics, e.g. voles were identified from

their relative tail length and birds that were plucked was identified to order or family from the size and shape of the feet or the beak. For two of the nests it was difficult to identify the prey to species (see above). Avian prey was identified by Vidar Selås, who also gave a second opinion on other prey when needed.

Because it was difficult to identify shrews (*Sorex spp*) to species on video, they were pooled as one prey type. It was also difficult to distinguish between field voles and root voles on the video clips, and therefore they were pooled as *Microtus* voles. It was also difficult to distinguish between *Microtus* voles and grey-sided voles (*Myodes rufocanus*) on the video clips, and it is possible that some prey identified as *Microtus* voles in fact were grey-sided voles, but they are rare in the study area (G.A. Sonerud, pers. comm.). It was also sometimes difficult to distinguish between *Microtus* voles and bank voles (*Myodes glareolus*), and in those cases they were pooled as a prey type termed “*Microtus* vole or bank vole”.

Some of the delivered prey were not identifiable at all, either due to their condition (e.g. decapitated, eaten at, skinned or plucked, or consisting of only a piece of a prey), or because they were hidden under the female hawk owl or hidden by the nestlings. These prey were registered as unidentified prey. Sometimes a parent bird arrived at the nest with a prey without delivering it, and instead flew off with it. If the same species and body characteristics (could have been eaten at) arrived within half an hour it was regarded as the same prey.

For each prey delivered at the nest, the following variables were registered if possible. 1) The sex of the parent that delivered the prey was as female if it fed the nestlings, because in owls, only the female feeds the nestlings (Cramp 1985; Kertell 1986; Olsen et al. 2013). If the nestlings fed unassisted or it could not be determined if they were fed, I identified the parental hawk owl by the wear of tail, because the females had a more worn tail than the males (pers.obs.). 2) Whether the nestlings were fed by the female or the nestling fed unassisted (without any preparation by the female). 3) Whether the prey was given to the female or directly to the nestlings if the parent delivery prey was the male. 4) Whether the prey was decapitated prior to delivery or whether it was eaten at other places than the head prior to delivery. 5) Handling time was measured for those recordings that included the moment when the first piece of a prey was given to a nestling and the moment when the last piece of the prey was ingested by a nestling (or female). If the nestling fed unassisted, the handling time was from when the nestling had the prey for itself to when it had been ingested. For each

handling time, number of pauses and length of each pause was measured. A pause was defined as a period when the female did nothing with the prey (female as feeder) for at least 5 s or when the nestling left the prey and did not touch it during at least 5 s. Handling time recordings were also classified by how many clips they consisted of.

Gross prey body mass was defined as the mass of a prey when it was captured by the hawk owl. Although there is intraspecific variation in body mass, I estimated body mass for each prey based on the average for each species. Estimates of gross prey body mass of shrew, northern birch mouse (*sicista betulina*), bank vole, *Microtus* voles and Norway lemming (*Lemmus lemmus*) were obtained from specimen trapped at the snap trapping site 40 km SE of my study area, in spring (Geir A. Sonerud, unpubl. data). Gross prey body mass of birds, frog (*Rana sp*), red squirrel (*Sciurus vulgaris*) and stoat (*Mustela erminea*) were obtained from the literature (Wauters & Dhondt 1989; Piontek et al. 2015; Stave 2016). The mass of the prey type “*Microtus* vole or bank vole” was calculated from the ratio between identified *Microtus* voles and bank vole among prey delivered, separately for each nest. Corresponding by the body mass of unidentified microtines were calculated from the ratio between Norway lemmings, *Microtus* voles, bank voles and “*Microtus* vole or bank vole” among prey delivered, separately for each nest. The body mass of an unidentified mammal was calculated from the ratio between shrews, northern birch mouse, Norway lemmings, *Microtus* voles, bank voles, “*Microtus* vole or bank vole” and unidentified microtines among prey delivered, separately for each nest. Finally, the body mass of unidentified prey was calculated from the ratio between all prey items delivered separately for each nest. Net prey body mass was defined as the mass of a prey item as it was delivered to the nest and due to high uncertainty of this estimate, I only used it for whole and decapitated mammals. It differed from gross prey body mass in the cases that mammals were decapitated prior to delivery, and I subtracted 16.5 % from the gross prey body mass (Asakskogen 2003).

## Statistical analysis

All statistical analysis were conducted with the software R, version 3.4.3 (R Development Core Team 2017). Figures 2-7 were constructed with R, while figures 1a, 1b, 5a and 5b were constructed with Microsoft Excel (version 2016). In R, packages “lme4”, “AICcmodavg”, “MASS” and “nlme” were used to analyse the raw data. Standard criterion of statistical significance was set to  $\alpha < 0.05$ . I used AIC to find the best fitted model. I kept the model if  $\Delta AICc > 2.0$ . If  $\Delta AICc < 2.0$ , I kept the simplest model. Estimates are shown as their mean  $\pm$  standard error (SE).

Generalised linear mixed models were used on all tests, with nest ID as random effect to control for repeated measurements of the same breeding pair and variation between breeding pairs (Pinheiro & Bates 2000). Logistic mixed effects regression by likelihood ratio was used to test for effect of the following response variables: the probability of at least one prey being delivered within a specific hour block, the probability that a prey was delivered by the female rather than the male, the probability that a prey delivered at the nest was a bird, the probability that a prey (small mammal) delivered at the nest was a Norway lemming, the probability that a prey (small mammal) delivered at the nest was a *Microtus* vole, the probability that a prey (small mammal) delivered at the nest was a bank vole, the probability that a prey delivered was decapitated prior to delivery, and the probability that a nestling handled a prey item unassisted. Linear mixed effects regression was used to analyse the number of prey per nestling per day as a function of nestling age, the number of prey delivered at the nest per day as a function of number of nestlings in the nest, handling time as a function of nestling age, and mass per piece of a prey fed by the female as a function of nestling age.

To analyse the probability of at least one prey was delivered to the nest within a specific hour block. For the diel activity pattern of the hawk owl, periodic components of the time series were set to sine and cosine functions, as suggested by Pita et al (2011). All days were divided into 24 hours blocks from 0-24, which was the explanatory variable (“time of the day”). This was corrected with hours in the video monitoring that were missing due to e.g. a full memory card. If one or more prey were delivered to the nest within a certain hour block, the score was “yes”. An hour block without prey deliveries was scored as “no”. Because of systematic error at Nest 3 (see above), only three of the nests were used in this analysis. Four cosinor models were tested for activity rhythm. M0 included only the random effect (Nest ID =  $\epsilon$ ) with no



peaks and is the average prey deliveries during a day. M1 is based on one peak during a day, M2 is based on two peaks during a day, and M3 is based on three peaks during a day. A model which has more than three peaks a day gives a blurred image of the diel activity pattern (R. Steen, pers. comm.).

List of cosinor models tested:

$$M_0: \text{logit}(f(x)) = a_0 + \varepsilon$$

$$M_1: \text{logit}(f(x)) = a_0 + \left( a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \varepsilon$$

$$M_2: \text{logit}(f(x)) = a_0 + \left( a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left( a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24} \right) + \varepsilon$$

$$M_3: \text{logit}(f(x)) = a_0 + \left( a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left( a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24} \right) + \left( a_3 \cos \frac{3*2\pi x}{24} + b_3 \sin \frac{3*2\pi x}{24} \right) + \varepsilon$$

In tests of the probability that a prey item was delivered by the female rather than the male, explanatory variables tested were nestling age, gross prey body mass, and class (mammal or bird) separately and together. In tests of the probability that a prey item delivered at the nest was a bird rather than a mammal, explanatory variables tested were nestling age and season separately and together. Amphibians was excluded from the tests, because only one frog was delivered. I used season as explanatory variable on the probability tests on small mammals and I only included identified *Microtus* vole, bank vole, Norway lemming and shrew. For the probability of Norway lemming I also included “*Microtus* vole or bank vole” in the test. Shrew were not tested because they were too few. In tests of the probability that a prey item delivered was decapitated prior to delivery, explanatory variables tested were nestling age and gross prey body mass separately and together. Because mammals and birds differ in body size for the same body mass, I separated them. Birds were not tested due to low sample size. In tests of the probability that a nestling handled a prey item unassisted, explanatory variables tested were nestling age, number of nestlings, net prey body mass (whole and decapitated mammals) separately and together.

In the Statistical test of number of prey per nestling per day as a function of nestling age, I used number of prey per nestling per day because the hawk owl is a specialist on microtines, and therefore the prey are fairly similar in size, and because it was difficult to estimate net prey body mass. This test was conducted only on data from complete days with recording, and when none of the nestlings had fledged during that day. I excluded nest 3 due to the

systematic recording error (see above). The same was done in the analysis of number of prey delivered at the nest per day as a function of number of nestlings in the nest. Prey delivered at the nest per day was  $\log_{10}$  transformed to get normal distributed residuals. Analysis of handling time was conducted for mammals, female as feeder, prey with known decapitating status (“yes” or “no”), prey not eaten at (except for decapitation) and video clip series with start and end of feeding. To explain handling time, explanatory variables tested were net prey body mass (whole or decapitated mammals), nestling age and number of nestlings, separately and together. Handling time and net prey body mass was  $\log_{10}$  transformed to get normal distributed residuals. The test of mass per piece of a prey fed by the female as a function of nestling age, included the same variables as the test of handling time, but was restricted to cases where feeding of a prey was included in one video clip and where it was possible to count pieces being fed. Mass per piece of a prey fed by the female was  $\log_{10}$  transformed to get normal distributed residuals.

## Results

### Diet

In total 680 prey items were recorded as delivered at the four hawk owl nests (tables 2, 3). Of these items, 414 were determined to species (including the prey categories as *Microtus* voles, “*Microtus* vole or bank vole”, and *Turdus* sp.), 110 to family, 21 to order and 50 to class, while 85 prey items were registered as unidentified prey.

Total gross body mass of prey delivered at the nests was estimated to 23016.8 g. The average estimated gross prey body mass was  $33.9 \pm 0.3$  g (N = 680, 4 nests). Estimated average gross prey body mass for mammals and birds were  $34.4 \pm 0.3$  g (N = 568) and  $23.0 \pm 4.7$  g (N = 26), respectively. For nest 1, the estimated average gross prey body mass was  $32.3 \pm 0.7$  g (N = 87). For nest 2, the estimated average gross prey body mass was  $37.5 \pm 1.1$  g (N = 113). For nest 3, the estimated average gross prey body mass was  $32.1 \pm 0.7$  g (N = 199) and for nest 4, the estimated average gross body mass was  $34.1 \pm 0.1$  g (N = 281). The largest amount of prey delivered in one day by number (40) and by gross prey body mass (1355 g) was recorded at nest 4 when the oldest nestling was 21 days.

Mammals were the most common prey by number and by gross prey body mass, making up 95.5 % and 96.9 %, respectively, when excluding unidentified prey. Of the mammals, the microtine family was the most common prey by number and by gross prey body mass, making up 92.8 % and 94.5 %, respectively, when excluding unidentified prey and unidentified mammals. Of the microtines, *Microtus* voles were in total the most common prey by number and by gross prey body mass, making up 68.0 % and 70.4 %, respectively, when excluding unidentified prey, unidentified mammals, unidentified microtines, and prey identified as “*Microtus* vole or bank vole”. At nest 2, Norway lemming was the most common prey both by number and by gross prey body mass. Birds constituted in total 4.4 % by number and 3.0 % by gross prey body mass of identified prey items. At nest 3 the number and mass of birds delivered was highest and constituted 9.8 % by number and 6.6 % by gross prey body mass of identified prey items.

Table 2. Prey items recorded delivered (number and percentage) at four hawk owl nests in southern Norway in 2014 (nest 4) and 2017 (nest 1, nest 2 and nest 3).

Prey category	Nest 1		Nest 2		Nest 3		Nest 4		All nests	
	N	%	N	%	N	%	N	%	N	%
Shrew (Soricidae)	0	0	1	0.9	2	1.0	5	1.8	8	1.2
Stoat ( <i>Mustela erminea</i> )	0	0	2	1.8	0	0	0	0	2	0.3
Red squirrel ( <i>Sciurus vulgaris</i> )	0	0	1	0.9	0	0	0	0	1	0.1
Northern birch mouse ( <i>Sicista betulina</i> )	0	0	1	0.9	0	0	0	0	1	0.1
Bank vole ( <i>Myodes glareolus</i> )	6	6.9	5	4.4	16	8.0	0	0	27	4.0
Norway lemming ( <i>Lemmus lemmus</i> )	0	0	49	43.4	4	2.0	0	0	53	7.8
<i>Microtus sp.</i>	21	24.1	48	42.5	105	52.7	79	28.1	253	37.2
Microtus vole or bank vole	21	24.1	0	0	38	19.1	6	2.1	65	9.5
Unidentified microtine ( <i>Arvicolidae</i> )	19	21.8	2	1.8	6	3.0	81	28.8	108	15.9
Unidentified mammal	4	4.5	1	0.9	4	2.0	41	14.6	50	7.4
<b>Total Mammals</b>	<b>71</b>	<b>81.6</b>	<b>110</b>	<b>97.3</b>	<b>175</b>	<b>87.9</b>	<b>212</b>	<b>75.4</b>	<b>568</b>	<b>83.5</b>
Meadow pipit ( <i>Anthus pratensis</i> )	0	0	1	0.9	0	0	0	0	1	0.1
Willow warbler ( <i>Phylloscopus trochilus</i> )	0	0	0	0	1	0.5	0	0	1	0.1
Thrush ( <i>Turdus sp.</i> )	0	0	0	0	2	1.0	0	0	2	0.3
Finch (Fringillidae)	0	0	0	0	0	0	1	0.4	1	0.1
Unidentified small passerine	2	2.3	1	0.9	16	8.0	1	0.4	20	2.9
Unidentified large passerine	1	1.1	0	0	0	0	0	0	1	0.1
<b>Total Birds</b>	<b>3</b>	<b>3.5</b>	<b>2</b>	<b>1.8</b>	<b>19</b>	<b>9.5</b>	<b>2</b>	<b>0.7</b>	<b>26</b>	<b>3.8</b>
Frog ( <i>Rana sp.</i> )	0	0	1	0.9	0	0	0	0	1	0.1
Unidentified prey	13	14.9	0	0	5	2.5	67	23.8	85	12.5
<b>Grand total</b>	<b>87</b>		<b>113</b>		<b>199</b>		<b>281</b>		<b>680</b>	

Table 3. Estimated gross prey body mass (g) of prey items recorded delivered at four hawk owl nests in southern Norway in 2014 (nest 4) and 2017 (nest 1, nest 2 and nest 3), with percentages by gross prey body mass separated for each nest and in total.

Prey category	Nest 1		Nest 2		Nest 3		Nest 4		All nests	
	g	%	g	%	g	%	g	%	g	%
Shrew (Soricidae)	0	0	10.0	0.2	20.0	0.3	50.0	0.5	80.0	0.4
Stoat ( <i>Mustela erminea</i> )	0	0	200.0	4.7	0	0	0	0	200.0	0.9
Red squirrel ( <i>Sciurus vulgaris</i> )	0	0	100.0	2.4	0	0	0	0	100.0	0.5
Northern birch mouse ( <i>Sicista betulina</i> )	0	0	10.0	0.2	0	0	0	0	10.0	0.04
Bank vole ( <i>Myodes glareolus</i> )	132.0	4.7	110.0	2.6	352.0	5.5	0	0	594.0	2.6
Norway lemming ( <i>Lemmus lemmus</i> )	0	0	1960.0	46.3	160.0	2.5	0	0	2120.0	9.2
<i>Microtus sp.</i>	735.0	26.2	1680.0	39.7	3675.0	57.6	2765.0	28.8	8855.0	38.5
Microtus vole or bank vole	674.1	24.0	0	0	1265.4	19.8	210.0	2.2	2149.5	9.3
Unidentified microtine ( <i>Arvicolida</i> )	609.9	21.7	73.4	1.7	201.0	3.1	2835.0	29.6	3719.3	16.2
Unidentified mammal	128.4	4.6	36.2	0.9	134.0	2.1	1406.3	14.7	1704.9	7.4
<b>Total Mammals</b>	<b>2279.4</b>	<b>81.1</b>	<b>4179.6</b>	<b>98.7</b>	<b>5807.4</b>	<b>91.0</b>	<b>7266.3</b>	<b>75.8</b>	<b>19532.7</b>	<b>84.9</b>
Meadow pipit ( <i>Anthus pratensis</i> )	0	0	20.0	0.5	0	0	0	0	20.0	0.1
Willow warbler ( <i>Phylloscopus trochilus</i> )	0	0	0	0	9.0	0.1	0	0	9.0	0.04
Thrush ( <i>Turdus sp.</i> )	0	0	0	0	180.0	2.8	0	0	180.0	0.8
Finch (Fringillidae)	0	0	0	0	0	0	22.0	0.2	22.0	0.1
Unidentified small passerine	30.0	1.1	15.0	0.4	228.0	3.6	15.0	0.2	288.0	1.3
Unidentified large passerine	80.0	2.8	0	0	0	0	0	0	80.0	0.4
<b>Total Birds</b>	<b>110.0</b>	<b>3.9</b>	<b>35.0</b>	<b>0.8</b>	<b>417.0</b>	<b>6.5</b>	<b>37.0</b>	<b>0.4</b>	<b>599.0</b>	<b>2.6</b>
Frog ( <i>Rana sp.</i> )	0	0	20.0	0.5	0	0	0	0	20.0	0.1
Unidentified prey	419.9	14.9	0	0	160.5	2.5	2284.7	23.8	2865.1	12.4
<b>Grand total</b>	<b>2809.3</b>		<b>4234.6</b>		<b>6384.9</b>		<b>9588.0</b>		<b>23016.8</b>	

## Relationship between number of prey items and number and age of nestlings

At nest 1 with seven nestlings the rate of prey deliveries per hour was 0.62 when the oldest nestling was from 15 to 19 days old, equivalent to 1 hour 37 minutes between each prey delivery. At nest 2 with six nestlings the rate of prey deliveries per hour was 1.01 when the oldest nestling was from 18 to 22 days old, equivalent to 59 minutes between each prey delivery. At nest 4 with eight nestlings the rate of prey deliveries per hour was 1.45 when the oldest nestling was from 20 to 23 days old and all nestlings were still in the nest, equivalent to 41 minutes between each prey delivery. For nest 3, delivery rate could not be estimated due to a systematic recording error (see method). Estimated mean number of prey per nestling per day was  $4.0 \pm 0.5$  ( $N=11$  days, oldest nestling 16-23 days old). If the net prey body mass (mass of prey delivered at the nest) was set equal to the average gross prey body mass (33.9 g), the average mass ingested per nestling would be 137 g per day late in the nestling period. There was a significant increase in number prey items per nestling per day with increasing nestling age (figure 1). There was also a significant increase in number of prey delivered at the nest per day with increasing number of nestlings in the nest (figure 2).

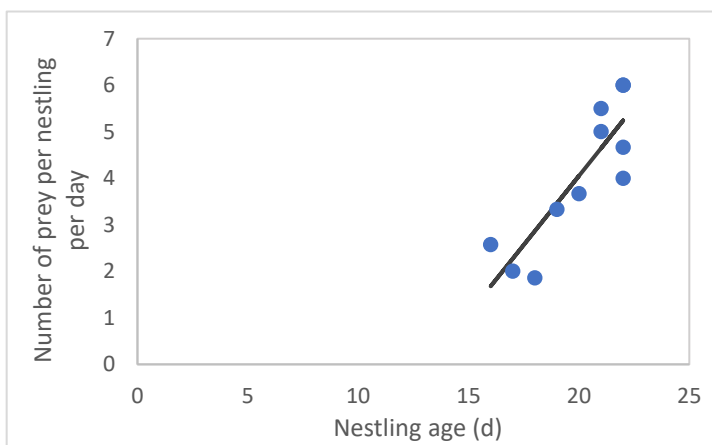


Figure 1. *Number of prey items delivered at the nest per nestling per day as a function of nestling age.*  $\beta_0 = -7.82 \pm 2.35$ ,  $\beta_1 = 0.59 \pm 0.117$ ,  $p = 0.0014$ ,  $N = 11$ , 3 nests.

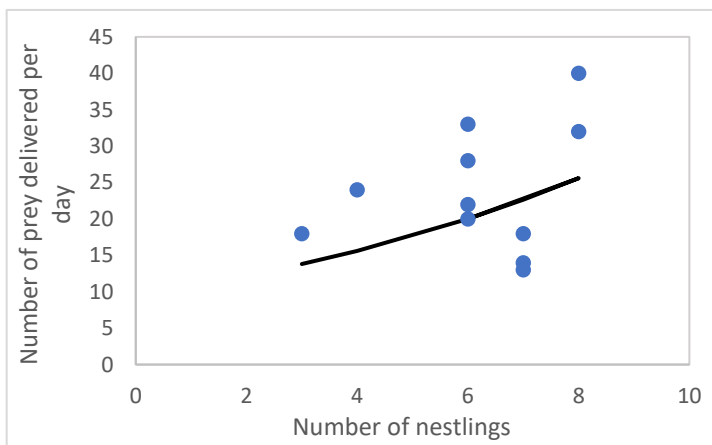


Figure 2. *Number of prey items delivered at the nest per day (back transformed from  $\log_{10}$ -transformed) as a function of number of nestlings in the nest.*  $\beta_0 = 0.98 \pm 0.13$ ,  $\beta_1 = 0.05 \pm 0.012$  (log-scale),  $p = 0.0037$ ,  $N = 11$ , 3 nests.

## Prey deliveries as a function of time of the day

Based on analysis of four types of cosinor models, the probability that a prey item delivered at the nest as a function of time of the day (24 hours blocks) was best explained by model 3 (table 4).

*Table 4. Model selection among four types of cosinor models based on AICc. The models explain the probability that a prey was delivered at a hawk owl nest (N = 3) as a function of time of day. See Appendix 2 and 3 for raw data used and output summary of best model.*

Model	K	AICc	$\Delta$ AICc
3	8	773.60	0.00
0	2	775.80	2.20
2	6	777.96	4.36
1	4	778.14	4.54

The average probability of at least one prey delivery at the nest within an hour during a day (24 h) was 0.57 (the midline estimating statistic of rhythm, abbreviated as MESOR), represented by model 0 with only the random effect included (Figure 3). Based on model 3, the probability of at least one prey being delivered at the nest per hour-block was highest in the evening right before sunset, within the 21-22 hour-block, with a probability of 0.68. Another peak occurred in the morning right after sunrise, within the 06-07 hour-block, with a probability of 0.67. In the afternoon there was a less clear third peak within the 14-15 hour-block, with a probability of 0.63. The lowest value was within the 01-02 hour-block, with a probability of 0.39. Overall the model 3 indicates that the hawk owls were active and hunting throughout the day, and that the main activity period is at daytime between 04:00 and 23:00 hours. See Appendix 3a-c to see the rate of prey deliveries for each hour-block separated for each nest. The high activity of prey deliveries at the morning starts within 03-04 hour block.

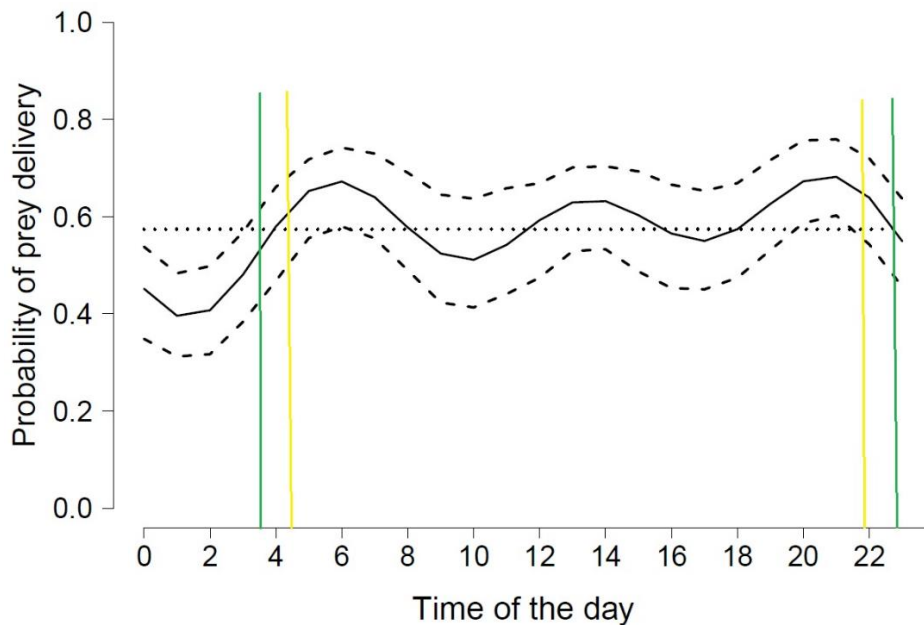


Figure 3. Generalized linear mixed model (model 3 from the cosinor analysis, see table 4) of the probability that at least one prey delivery occurred within an hour-block at a hawk owl nest as a function of time of the day, represented by the solid black line. The 95% confidence interval is represented by the two dashed lines. The dotted line is the midline estimating statistic of rhythm (MESOR). Vertical yellow lines represent time of sunrise and sunset on 13 May (shortest day during the study), while vertical green line represent time of sunrise and sunset on 23 June (longest day during the study). Based on 568 hour-blocks recorded by video at 3 nests. See Appendix 2 and 3 for the raw data and output summary.

## Prey deliveries by male and female

The parent delivering the prey item was determined for 580 prey items delivered at the four nests. The female delivered most of the prey items recorded (91 %). Most of the prey items delivered by the male (N=53) were delivered when the nestlings were young (figure 4). All prey items recorded delivered by the male were given to the female while she was present in the nest, except for a case where the male gave a whole *Microtus* vole to an 18 days old nestling who swallowed it, while the female was present in the nest. The probability that a prey item was delivered by the female increased significantly with nestling age. When the oldest nestling in the nest was 15 days old or more, the probability that a prey delivered by the female was  $> 0.5$ . Neither class (bird or mammals), gross prey body mass, or relevant interactions had any significant effect on the probability that a prey item was delivered by the female.

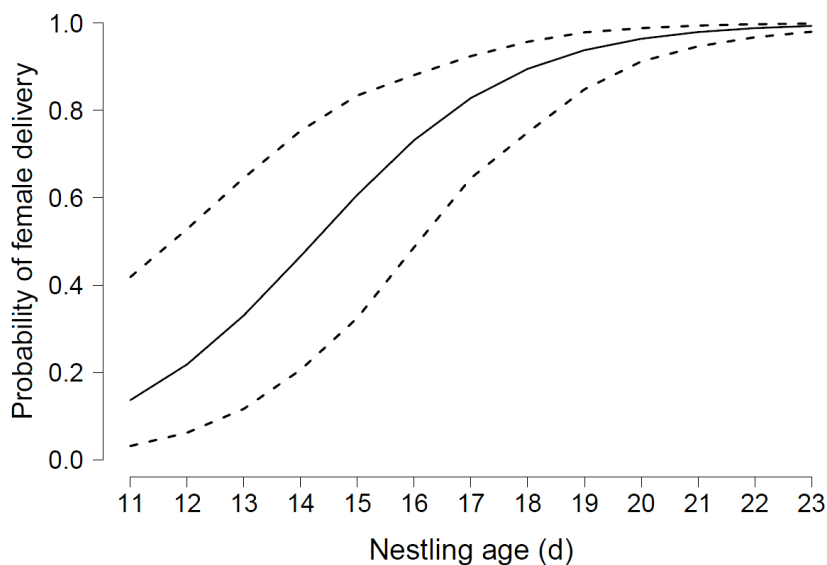


Figure 4. The probability that a prey item delivered at a hawk owl nest was delivered by the female as a function of nestling age. The 95% confidence interval is represented by the two dashed lines.  $\beta_0 = -8.113 \pm 1.607$ ,  $\beta_1 = 0.569 \pm 0.081$ ,  $p = 0.001$ ,  $N = 580$  prey items, 4 nests.



## Deliveries of birds as a function of season

Explanatory variables tested to explain the probability of a prey delivered at the nest was a bird rather than a mammal was season and nestling age separately and together. The  $\Delta AICc$  was not greater than two between any of the three models (Table 5). I chose the model with only season as the best fitted model to explain the probability of a prey delivered at the nest was a bird rather than a mammal because of the lowest AICc (204.85) and the lowest p-value ( $p = 0.062$ ) (figure 5). The probability of a prey item delivered being a bird rather than mammal increased marginally non-significant throughout the season. The probability of a prey being a bird increased from 0.008 on 13 May (first day of recording) to 0.05 on 9 June (last day of recording). Number and mass of birds delivered was higher at nest 3 than at the other nests (tables 2, 3).

Table 5. Model selection based on AICc to best explain the probability of a prey delivered at the hawk owl nest being a bird rather than a mammal.

Model	K	AICc	$\Delta AICc$	Explanatory variables
3	3	204.85	0.00	Season
1	3	206.24	1.39	Nestling age
2	4	206.67	1.82	Season + Nestling age

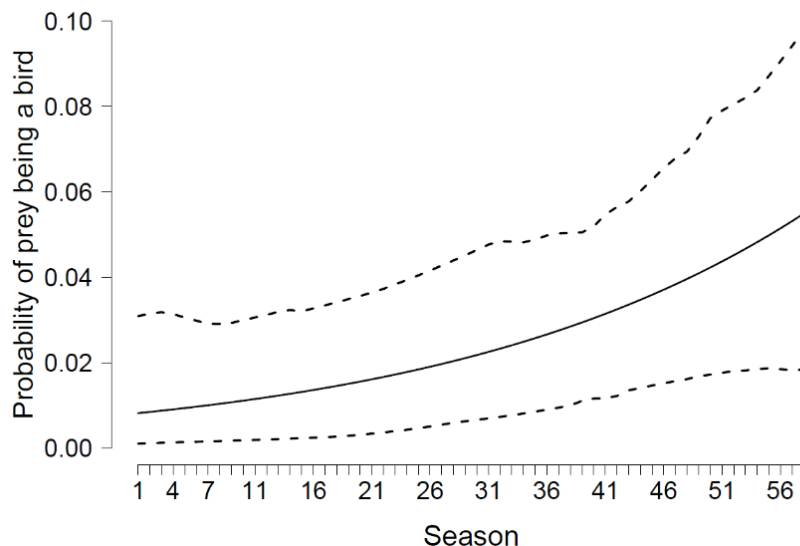


Figure 5. The probability that a prey delivered at the nest was a bird rather than a mammal as a function of season. See fig. 4 for further explanation. For the variable season, 1 denotes 13 May (first day of recording) and 58 denotes 9 June (last day of recording).  $\beta_0 = -4.46 \pm 0.73$ ,  $\beta_1 = 0.034 \pm 0.018$ ,  $p = 0.062$ ,  $N = 594$  prey items, 4 nests.

## Deliveries of small mammals as a function of season

Of 680 prey items recorded, were 341 prey items identified as either *Microtus* vole, bank vole or Norway lemming. In addition, 65 prey items were identified as a “*Microtus* vole or bank vole”. The probability of a prey item delivered being a Norway lemming rather than another small mammal increased significant throughout the season (figure 6a). The probability of prey being a Norway lemming changed from 0.0001 on 13 May (first day of recording) to 0.20 on 9 June (last day of recording). There was no significant effect of season on the probability of a prey being a *Microtus* vole rather than another small mammal, or on the probability of prey being a bank vole rather than another small mammal (Figure 6b, 6c). Numerically, the probability that a prey was a *Microtus* vole decreased with season, and for the bank vole it was stable low throughout the season.

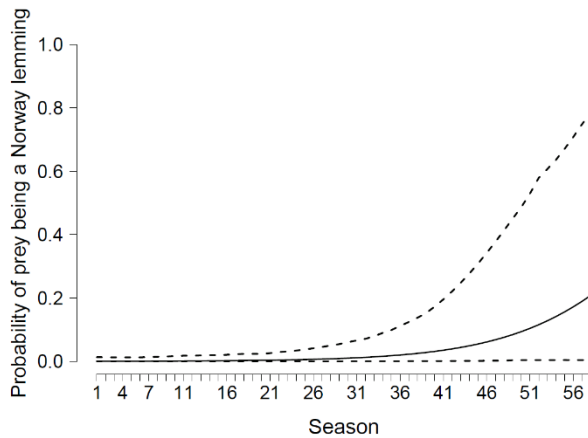


Figure 6a. The probability that a prey delivered at a hawk owl nest was a Norway lemming rather than another small mammal as a function of season. See fig. 4 for further explanation.  $\beta_0 = -8.08 \pm 2.54$ ,  $\beta_1 = 0.12 \pm 0.05$ ,  $p = 0.029$ ,  $N = 406$  prey items, 4 nests.

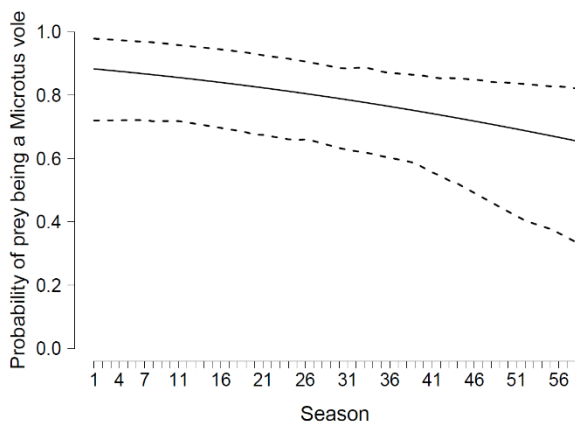


Figure 6b. The probability that a prey delivered at a hawk owl nest was a *Microtus* vole rather than another small mammal as a function of season. See fig. 4 for further explanation.  $\beta_0 = 2.05 \pm 0.76$ ,  $\beta_1 = -0.03 \pm 0.02$ ,  $p = 0.24$ ,  $N = 341$  prey items, 4 nests.

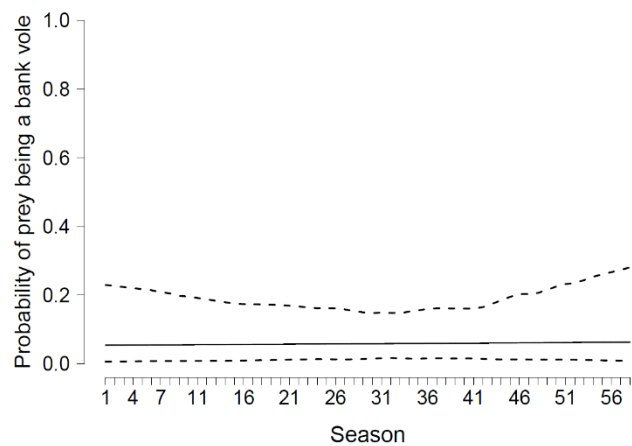


Figure 6c. The probability that a prey delivered at a hawk owl nest was a bank vole rather than another small mammal as a function of season. See fig. 4 for further explanation.  $\beta_0 = -2.87 \pm 1.15$ ,  $\beta_1 = 0.003 \pm 0.03$ ,  $p = 0.93$ ,  $N = 341$  prey items, 4 nests.

## Prey handling prior to delivery at the nest

For 268 of 568 prey items identified as a mammal delivered at the hawk owl nests, it was possible to determine whether or not the item was decapitated prior to being delivered.

Among these 117 were registered as decapitated. The best model to explain the probability of a prey being decapitated prior to delivery included only gross prey body mass (table 6), but the  $\Delta AICc$  value were  $< 2$  compared to the model that included nestling age. I chose the first (model 3) because it was a simpler model and because nestling age did not explain the probability of decapitation significantly, neither with prey mass nor alone. The probability of a prey being decapitated prior to delivery increased significantly with prey mass (Figure 7).

Table 6. Model selection based on AICc to best explain the probability that a prey (mammal) being decapitated prior to delivery at a hawk owl nest.

Model	K	AICc	$\Delta AICc$	Explanatory variables
3	3	362.51	0	Prey mass
1	4	362.75	0.24	Nestling age + prey mass
2	3	370.22	7.72	Nestling age

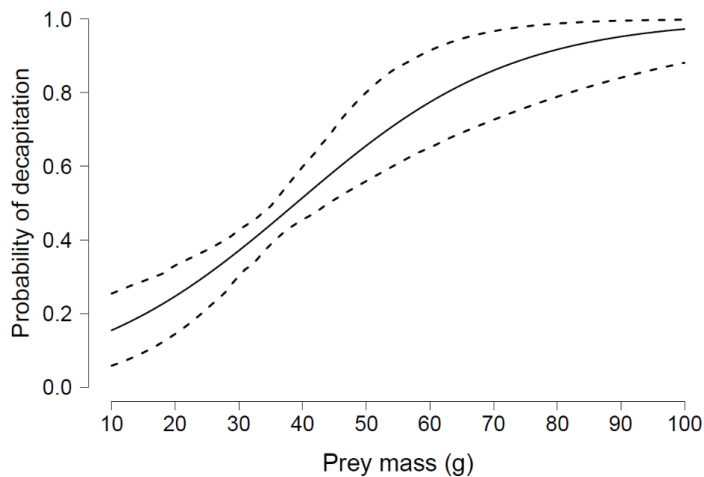


Figure 7. The probability that a prey (mammal) being decapitated prior to delivery at a hawk owl nest as a function of prey body mass (based on model 3 in table 6). See fig. 4 for further explanation.  $\beta_0 = -2.29 \pm 0.79$ ,  $\beta_1 = 0.058 \pm 0.023$ ,  $p = 0.009$ ,  $N = 268$  prey items, 4 nests.

## Prey handling in the nest

Whether a nestling handled a prey item unassisted or was fed by the female was registered for 587 prey items. The female fed the nestlings in 92.8 % of the cases. The lowest age at which a nestling was recorded to handle a prey item unassisted was when it was 18 days old, and the prey was a decapitated *Microtus* vole. In nest 3 there was no recorded case of a nestling feeding unassisted (N=177). Avian prey were never handled by a nestling unassisted. There was no registered case where the female or the male left a prey in the nest for the nestlings to ingest unassisted. Neither age of nestlings, number of nestlings, nor any relevant interaction had any significant effect on the probability that a prey was handled by a nestling unassisted. Numerically, the probability that a prey was handled by a nestling unassisted increased with age of the nestlings ( $\beta_1 = 0.14 \pm 0.10$ ) and decreased with number of nestlings ( $\beta_1 = -0.12 \pm 0.10$ ), but this was not significant ( $p = 0.19$  and  $p = 0.25$ , respectively). Due to a high uncertainty of the net prey body mass, I included only whole and decapitated mammalian prey (net prey body mass). Numerically, the probability of a nestling feeding unassisted on mammalian prey decreased with increasing net prey body mass ( $\beta_1 = -0.12 \pm 0.11$ ,  $p=0.28$ , N=135 prey items, 4 nests). The model predicted that there was a probability of 0.07 of a prey being handled unassisted by nestling at an age of 23 days. The switch (probability > 0.5 of a nestling feeding unassisted) was at an age of 43 days. Because this prediction is beyond my data, it is uncertain as reflected by the wide confidence interval (figure 8).

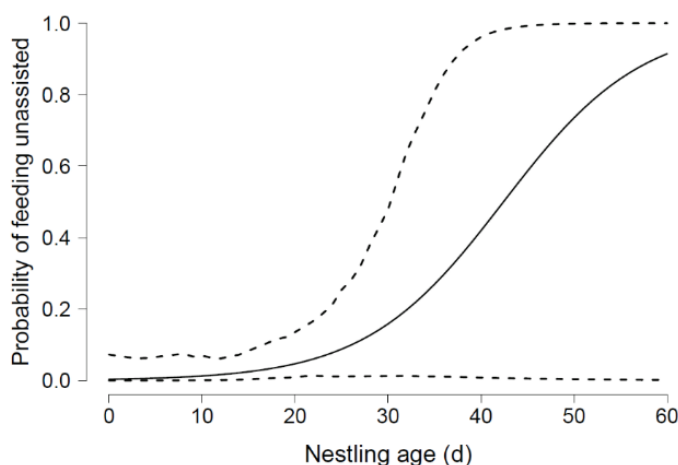


Figure 8. *The probability that a hawk owl nestling handled a prey item unassisted as a function of nestling age. See fig. 4 for further explanation. Nestling ages <11 and >23 are beyond my data.  $\beta_0 = -5.71 \pm 2.29$ ,  $\beta_1 = 0.14 \pm 0.10$ ,  $p = 0.19$ ,  $N = 587$  prey items, 4 nests.*

## Prey handling time

When the female fed the nestlings with a *Microtus* vole, average handling time was  $207.0 \pm 21.7$  s ( $N = 25$ ) for whole items and  $161.2 \pm 22.1$  s ( $N = 20$ ) for decapitated items. Handling time when the female fed the nestlings decreased marginally non-significant with nestling age (figure 9). I also tested the effect of number of nestlings and net prey body mass (whole and decapitated mammalian prey), both separately and together with nestling age, but those variables had no significant effect on handling time. I further tested whether mass per piece of a prey fed by the female was a function of nestling age. Indeed, mass per piece of a prey fed by the female increased significantly with the nestling age (figure 10). This suggests that the number of pieces per prey fed by the female decreased with nestling age. For each prey item, the size of each piece fed by the female varied a lot, but the last piece (normally the back of the prey) was in general the largest.

When the nestlings handled a prey item unassisted, they swallowed it whole in a few seconds ( $< 5$  s). In the 43 videoclips, where number of nestlings fed by the female was registered, all nestlings in the nest were fed by the female in 53.5 % of the cases, and when three or more nestlings were present in the nest, only in one case was only one nestling fed by the female. After the prey had been ingested, the female usually cleaned her beak by rubbing it against the inside walls of the nest-box. She also cleaned the bottom of the nest-box by eating any prey remains, feathers and pellets left by the nestlings.

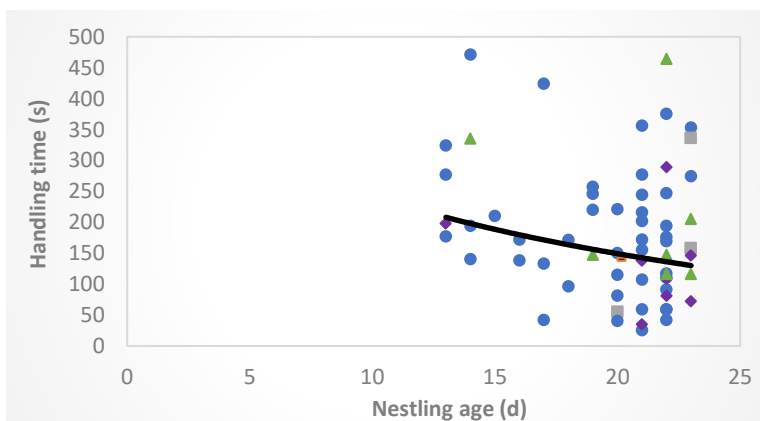


Figure 9. Handling time (back transformed from  $\log_{10}$ -transformed) when the female fed the nestlings as a function of nestling age. Blue circles = *Microtus* voles, purple diamond = “*Microtus* vole or bank vole”, green triangle = bank vole, grey square = Norway lemming and orange stripe = shrew.  $\beta_0 = 2.582 \pm 0.235$ ,  $\beta_1 = -0.020 = 0.012$  (log-scale),  $p = 0.088$ ,  $N = 64$ , 3 nests.

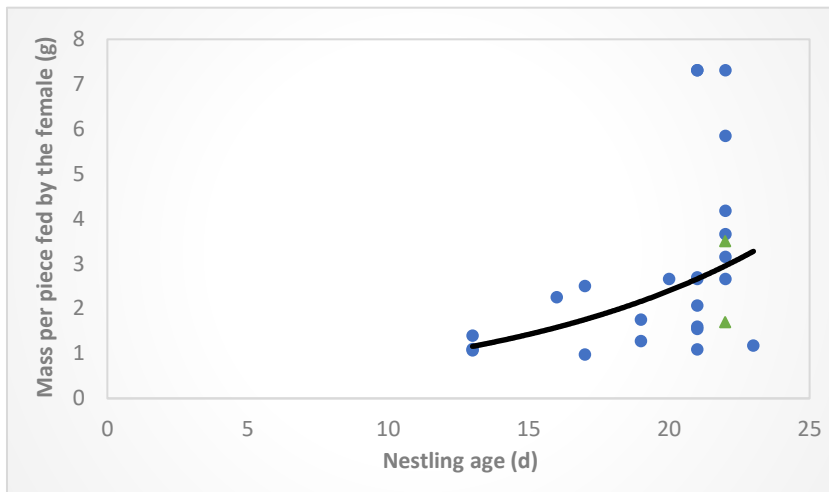


Figure 10. Mass per piece of a prey fed by the female (back transformed from  $\log_{10}$ -transformed) as a function of nestling age. Blue circles = *Microtus voles* and green triangle = bank vole.  $\beta_0 = -0.523 \pm 0.340$ ,  $\beta_1 = 0.045 \pm 0.016$  (log-scale),  $p = 0.009$ ,  $N = 26$  (all in nest 3).

## Discussion

### Diet

The prey items delivered at the nests in my study were by number 95.5 % mammalian, 4.4 % avian and 0.2 % amphibian of identified prey. Of mammalian prey delivered at the nest, microtines were the most common prey by number and by gross body mass, 92.8 % and 94.5 %, respectively of identified prey. The gross prey body mass varied from 9-100 g and the average prey was estimated to weight 34 g at capture. Other studies conducted in Fennoscandia on pellets and prey remains from hawk owls, also found that microtines are the most important prey, with an average of 96 % in number of the prey composition (Mikkola 1972, and references therein).

However, studies conducted on the subspecies of hawk owl in North America (*Surnia ulula caparoch*) found that the proportion of snowshoe hare (*Lepus americanus*) in the diet was up to 50 %, dependent on the stage of the hare cycle (Kertell 1986). Based on a study by Rohner et al. (1995) on pellets from breeding hawk owls in Canada, I estimated average prey body mass to be 69 g, which is more than twice of what I found. This expresses the opportunistic potential of the hawk owl, and that the diet of hawk owls in Fennoscandia is not only showing a preference for microtines, but also the high availability of microtines compared with other prey species (Rohner et al. 1995).

Of the microtines delivered at the nest in my study, *Microtus* voles were the most important prey by number and by gross prey body mass with, 68.0 % and 70.4 %, respectively (when excluding unidentified prey, unidentified mammal and unidentified microtines). Previous studies have shown that microtines of the Genera *Myodes* and *Microtus* are both important prey for the hawk owl in Fennoscandia (Mikkola 1972; Sonerud 1986). Northern red-backed vole (*Myodes rutilus*) is not found in my study area, while the grey-sided vole (*Myodes rufocanus*) is rare. The reason for the low proportion of bank vole in my study may be that only two of the nests were monitored when the ground was still snow covered, and for both nests the start of recording was late in the nestling period when the snow had started to melt. Thus, it is likely that the hawk owls, had already shift from hunting in the forest on bank voles when the snow covered the ground to hunting in open habitats on *Microtus* voles which were more available when the snow had started to melt (see Nybo & Sonerud 1990). This is

reflected in the stable low probability of bank vole as prey throughout the season. *Microtus* voles are heavier and have presumably the same handling time as bank voles. Therefore, *Microtus* voles are more profitable prey than bank voles and my result matches the optimal foraging theory that predators select prey to maximize net energy (Pyke 1984). Another important factor that affecting the utilization of a prey, is the probability of capture success, and because *Microtus* voles are slower than bank voles, it is therefore likely that *Microtus* voles are easier to capture for the hawk owl (see Nishimura & Abe 1988). The possible explanation of the numerical decrease in the probability of *Microtus* voles delivered to the nest, could be that the vegetation had become high and dense. Thus, *Microtus* may had become less available at the same time other species had become more accessible.

On 17 May in nest 4 (first day of recording), 40 prey items were recorded delivered at the nest, equivalent to five prey per nestling. The availability of prey would affect prey capture rate and the prey availability would be greatest in clear-cuts just after snow has disappeared and before vegetation leafs out (Jacobsen & Sonerud 1993). A possible explanation is that because 2014 was a peak year for microtines and 17 May was probably a day where the snow has disappeared and before the vegetation had started to leaf out.

Norway lemmings were delivered at two nests, and at nest 2 it was the most common prey. The probability of that a small mammal delivered at the nest being a Norway lemming increased throughout the season. While Norway lemming made up 8 % of the prey items in my study, Mikkola (1972) found that only 3 % of prey of hawk owls in Fennoscandia were lemmings. In fact, lemmings were rare prey to hawk owls at three of my nests. The reason for high proportion of Norway lemming in nest 2 could be that it was the nest with the highest altitude with good access to preferred habitats for the Norway lemming. The nest was also monitored late in the season. Thus, it is likely that a well-developed vegetation in clear-cuts had decreased the availability of the most profitable prey *Microtus* voles. It is possible that the hawk owls had shifted foraging habitat to a less-developed mountain vegetation and expanded the range of the diet (see Nybo & Sonerud 1990). Norway lemming are more likely to be in habitats with lower vegetation and they were slower than voles (Andersson 1976; Saetnan et al. 2009). There are two hypotheses that explain why many predators avoid to capture or eat Norway lemmings; cryptic colouration or aposematism. Andersson (2015) found that the reason for Norway lemming differing from those other microtines in colouration and behaviour was aposematism. Norway lemming are often only partly consumed by raptors



(Steen et al. 1997), and Hagen (1952) suggested they are tasting or smelling nasty. The choice of Norway lemmings can be regarded as a best-of-a-bad-job, a hungry predator will eat an aposematic prey if it contains sufficient nutrition (Halpin et al. 2014). Nest 2 was also the nest with the widest diet, but it can have a methodical cause, because this nest had the best camera setup and therefore the highest probability to identify prey items.

In total, only eight shrews were delivered at the nests, making up 1 % of the prey items recorded. That hawk owls take few shrews were also found by Mikkola (1972) and Nybo & Sonerud (1990). This correspond to the fact that hawk owls only breeds at high abundance of microtines, and the inclusion of alternative prey in the diet such as shrews will therefore be low. However due to travelling cost, single-prey loading predators selectively transport large prey at nest and small prey are more likely to be consumed at capture site (Bourne 1985; Sonerud 1989). Therefore, it is likely that I have underestimated shrews in the total prey composition of hawk owls during the breeding season in this study.

Avian prey occurred at all nests, but made up only 4 % of prey items delivered. Other studies have found that the proportion of birds during the breeding season posed a small part of the diet (Mikkola 1972; Cramp 1985; Rohner et al. 1995). Among 26 birds recorded, 19 were delivered at nest 3. The probability of a prey item delivered at the nest being a bird rather than mammal tended to increase throughout the season. A possible explanation of the high proportion of birds at nest 3 (9.5 %) may be that this nest was filmed late in the season, and therefore it was likely a well-developed vegetation in clear-cuts, which had decreased the availability of the most profitable prey *Microtus* voles (see Nybo & Sonerud 1990). On the other hand, late in the season (June/July) the abundance of vulnerable passerine nestlings and fledglings, and less attentive parents who are finding food for their offspring, would increase the availability of passerines for the hawk owl (see Selås 1993; Martin et al. 2000).

Examination of 14 stomachs of hawk owls during winter found that birds constituted 32% (Mikkola 1972). The higher proportion of birds in the diet during winter than during summer is probably due to the snow cover reduces the availability of microtines (Mikkola 1972; Sonerud 1986). Alternatively, the high proportion of birds during winter in the study by Mikkola could be that the hawk owls who were found or shot were close to settlement because they searched for new places to settle down after the microtines had broken down. Because nestling age did not affect the probability that an avian prey was delivered, while season tended to, hawk owls probably do not selectively choose prey after the nestlings need,

but rather capture birds because they are available. This further expresses the opportunistic potential of the hawk owl.

### **Relationship between number of prey items and number and age of nestlings**

I found that number of prey delivered per nestling increased with nestling age. Older nestlings are larger and therefore need more food, but growth rate are not constant and nestlings may need more energy when growth rate is highest (Grundel 1987; Barba et al. 2009; Steen et al. 2012). A Finnish study conducted by Huhtala et al. (1987) on hawk owl nestlings found that growth rate ceased after 17-18 days, and therefore it is likely the rate of food provisioning was highest at age of 17-18 days. Because I use the age of the oldest nestling in the nest as nestling age and because of the large age difference in the brood and the large brood size, I assume that the rate of provisioning in the nest is highest when the average age of nestlings are closest to 17-18 days and all nestlings still in the nest. That means that the larger the brood is, the less the average age will be for when the need of food is highest in the nest. Number of prey delivered at the nest was reduced after one nestling had fledged, but number of prey per nestling left in the nest increased with number of nestlings having fledged. The reason for this increase was probably that the reduction in rate of prey deliveries at the nest was delayed, relative to the fledgling of young.

I found an increase in number of prey delivered at the nest per day with increasing number of nestlings in the nest. Studies on other birds also found that food deliveries increased with number of nestlings (Nur 1984; Robinson & Hamer 2000), but not all parents can compensate for a large brood (Barba et al. 2009). On the other hand, larger broods gain thermal benefits and therefore need less energy (Royama 1966). In raptors, the young hatch asynchrony as an adaptation to a possible reduction of brood size as a response to lack of food (Slagsvold & Wiebe 2007). Because the cameras were set up late in the nestling period it is possible that this reduction already had happened. There was clearly less delivery of prey at nest 1, with seven nestlings, than at the other nests. My explanation is that there was a low availability of microtines during the three days of observations because the snow covered enough of the ground for the microtines to be able to hide. None of the nestlings died, so it apparently was enough food.

The rate of prey deliveries per hour was 0.62-1.45 (when oldest nestling 15-23 days old). Similarly, 0.8-2.5 prey deliveries per hour during daytime was found by Leinonen in 1978 (cited in Cramp 1985, p. 499). I used 24 hours, whereas Leinonen used only daytime, so my values would be expected to be lower (see below).

### **Diel activity pattern**

The hawk owls delivered most of the prey between sunrise and sunset. This correspond to the fact that Hawk owls are diurnal (Cramp 1985). The probability of at least one prey being delivered at the nest within an hour-block had two marked peaks during the day. The first was within the 06-07 hour-block right after sunrise, and the second was within the 21-22 hour-block and it was right before sunset. There was also a smaller peak within the 14-15 hour-block right after solar noon (c. 1315 p.m.). Fewer deliveries occurred around midnight (12-3 a.m.) and was lowest within 01-02 hour-block. A study conducted by Huhtala et al. (1987) on three hawk owl nests in northern Finland by use of an automatic recorder, found that there was a peak in nest visits early in the morning (3-4 a.m.) around noon (11 a.m-1 p.m.) and in the evening (8-11 p.m.), and fewer visits occurred 2-3 hours around midnight. This correspond well with my results. The reason for some differences between the two studies could be geographical differences (longer days in northern Finland), an automatic recorder counting all visits, and that the test that I use is conservative by testing only for the probability of at least one prey being delivered per hour-block. This test is better suited to species where the average rate of prey deliveries is less than one per hour.

The hawk owl uses the sight to locate the prey (Sonerud 1992b). A possible explanation for the drop in prey deliveries around midnight may therefore be the reduced hunting efficiency, although bank voles and *Microtus* voles are most active during night (R. Steen unpublished). It has also been found that microtines have short-term activity rhythm where they switch between active and rest phases, so they are also active during the daytime (Halle 2000). The reason for the peak in prey deliveries in the morning may be that as it started to be lighter, the efficiency of the hawk owls increased, whereas the activity of prey species were still high. Alternatively, the hawk owls increased the hunting activity to compensate the low delivery rate during the night to meet the need of the nestlings. The reason for the peak in deliveries in the evening may be that right before it get darker the hawk owls increased the hunting activity

to prepare for the night to meet the need of the nestlings. Alternatively, the activity of prey species were higher right before it started to be dark. The peak in the middle of the day was probably an increase in hunting activity by the hawk owls. It is important to be aware of the fact that what is being delivered have not necessarily been captured right before, because hawk owls are known to cache prey nearby the nest (Kertell 1986; Huhtala et al. 1987; Gniadek & Holt 2017).

The probability of delivering a prey at the nest was relatively high throughout the day and was reflected by the estimated number of four prey per nestling per day (late in the nestling period). If the net prey body mass was set equal to average gross prey body mass (34 g), the average mass ingested per nestling would be 137 g per day late in the nestling period. In comparison in the Ural owl and tawny owl, which are larger and has smaller brood size, it was 153 g/d and 56 g/d, respectively (Moen 2015; Stave 2016). This cannot be compared directly because I only have data from late in the nestling period when the need of food is highest. Huhtala et. al (1987) found that hawk owls visited their nest 3-4 times more than any of the other northern boreal owls. A study by Sonerud (1986) on non-nesting hawk owls, Eurasian kestrels and common buzzards, found that hawk owl was an effective hunter compared to the two other species. This was reflected in the breeding success in my study, where none of the nestlings died.

### **Prey deliveries by male and female**

The female delivered most of the prey recorded at the nest. All prey items delivered at nest by the male were given to the female, except for one case. Most of the prey items delivered by the male were delivered when the nestlings were young. The probability of prey delivered at nest by the female was  $> 0.5$  when the oldest nestling was 15 days old or more. Similar results were found by Kertell (1986) in Alaska, where the female brooded the young almost constantly the first 14 days and all hunting was done by the male, while after two weeks the food transfer happened outside of the nest. I observed many times that the female left the nest and returned with a prey within a minute. Probably the male has vocalized on a perch in vicinity of the nest to the female that he had food, alternatively she had retrieved a cached prey (Patrikeev 2006).

For raptors the female does most of the parental care at the nest, i.e. incubation, brooding and feeding nestlings, while the male provide food to the family and may be assisted by the female later in the nestling period (Sonerud et al. 2014). Asymmetric roles in raptors, may be an adaption to the conflict between time spent collecting and preparing food to nestlings (Sonerud et al. 2013). It is an optimization of spending the time efficiently in provisioning dependent nestlings (Sonerud et al. 2014).

The probability that the female delivered prey at nest increased with age of nestlings, may be because the older nestlings become less dependent of the female. Thus, she spends more time outside of the nest and is therefore more likely to intercept the male's provisioning outside of the nest and to have entirely control of allocation of prey items between self-feeding and feeding of nestlings (Kertell 1986; Patrikeev 2006; Sonerud et al. 2013).

### **Prey handling prior to delivery at the nest**

In my study, the hawk owls decapitated 44 % of the mammals prior to delivery at the nest.

The probability of a prey (mammal) being decapitated prior to delivery increased with prey body mass. Studies on the hawk owl by use of direct observations also found that some prey were decapitated before it was brought to the nest (Kertell 1986; Patrikeev 2006).

Also in the Eurasian kestrel and the tawny owl the probability of decapitation prior to delivery at the nest increased with prey body mass (Steen 2010; Stave 2016). For the Eurasian kestrel the probability of decapitation decreased with nestlings age for microtines, but not for avian prey, and in general the probability of decapitation was lower for mammalian prey compared to avian prey Steen (2010). Steen (2010) found that the reason for the decrease in the probability of decapitation of mammals was that the gape size and swallowing capacity increases with age and the nestlings would gradually be able ingest whole microtines, while birds were too large and were beyond the gap limitation regardless of nestling age. Sodhi (1992) found that merlins (*Falco columbarius*) were more likely to prepare prey at the capture site with increasing distance from their nest, probably to reduce flight cost.

Possible reason of why it was no effect of nestling age in my study, may be that the video recording started late in the nestling period, and it is therefore likely that the gap-size for the nestlings had developed sufficiently to be able to ingest head of microtines.

## Prey handling in the nest

Although nestling age, number of nestlings and net prey body mass did not have a significant effect. Numerically the probability that a prey was handled by a nestling unassisted increased with nestling age, and decreased with number of nestlings and net prey body mass. Birds were never handled by a nestling unassisted.

Numerically regarded these results agree with the feeding constraint hypothesis, because differences in the age of the nestlings lead to differences in size between the nestlings and therefore the need of maternal assistance increases with the size of prey (Slagsvold & Sonerud 2007). Sonerud et al. (2014) found on a study conducted on nine raptor species that the probability of feeding assistance by the female was higher for larger prey compared to smaller prey, was higher for birds than for mammals, and decreased with nestling age. A study conducted on the northern goshawk (*Accipiter gentilis*) found that when food was abundant, the female continued to feed the nestlings although they were capable of feeding unassisted, and the reason was that when food was abundant, the female could afford to desist from hunting and spend more time feeding the nestlings to optimise conditions to achieve a high breeding success by controlling the distribution of food and reduce the number of aggressive interactions between the nestlings (Byholm et al. 2011).

The model of whether a nestling handled a prey unassisted as a function of nestling age, predicted that the switch (probability  $> 0.5$  of nestlings feeding unassisted) was at an age of 43 days. Because the prediction is beyond my data, it is uncertain, as reflected by the wide confidence interval. Taxonomically, hawk owls are closest to *Glaucidium* owls (Ford 1967 (cited in Rohner et al. 1995)). Also Pygmy owl (*Glaucidium passerinum*) nestlings also rarely ingested prey items unassisted in the nest and the predicted switch was when the fledglings were 40 days old, a week after fledging (Sonerud et al. 2014). For the Tengmalm's owl and Ural owl, on the other hand, the switch was when the nestling was 21 days and 20 days, respectively (Sonerud et al. 2014).

The female fed the nestlings in 93% of the cases of prey delivery. The first time a nestling was recorded to handle a prey item unassisted was when the oldest nestling in the brood was 18 days and the handling time was then  $< 5$  s. A possible explanation for the extended female

confinement to the nest and even to fledging period in the hawk owl, even though the nestlings were capable to ingest unassisted. May be that hawk owls only breed at high abundance of prey. The female can then afford to desist from hunting and spend more time to distribute the food between the nestlings, contribute to reducing aggressive interaction between them, and prevent food being monopolized by dominant nestlings (Fargallo et al. 2003) and thereby increasing the chance of survival of youngest nestling. This is particularly important in hawk owls because they often have large clutches. For instance in nest 4 there were eight nestlings, corresponding to an age difference of about 2 weeks. In more than half of the cases, the female fed all nestlings in the nest from the same prey, and was often that the nestlings stood in a circle around the female and waited nicely for their turn to be fed (per.obs.).

### **Prey handling time**

There was a trend that handling time decreased with nestling age. I found that the reason for the decrease in handling time with nestling age was probable that mass per piece of a prey fed by the female, increased with nestling age. This may indicate that the female was capable of adjusting the size of the pieces of prey fed to the nestlings with the change in the age of the nestlings. Sonerud et al. (2014) found that handling time increased with prey body mass for five raptors. The reason for no effect of the prey body mass on handling time in my study, could be that the hawk owl is a specialist on microtines, and therefore a narrow diet and small mass differences between prey items. Also, because my mass estimates are average masses for each prey category, and the variation of the individual masses will not be reflected (e.g. juvenile vs. adult).

### **Conclusion**

My results have shown that the hunting activity of hawk owls in the breeding season are high. The hawk owl delivered prey at the nest at all hours and the probability of prey being delivered was high throughout the day, with two marked peaks, one after sunrise and one before sunset. Because the switch of a nestling to feed unassisted was not during the nestling period. It has been interesting for a future study to find out how old a fledgling is when the probability of feeding unassisted is  $> 0.50$ .

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## Appendix

**Appendix 1. Raw data used for analysis of prey delivery as a function of time of the day (n=3 nest). Used in table 4 and figure3.**

HOUR-BLOCK	PREY DELEVERIES	HOURS MONITORED
0	12	24
1	7	24
2	14	24
3	26	24
4	16	24
5	23	23
6	19	23
7	20	23
8	23	23
9	20	23
10	19	23
11	18	23
12	17	24
13	19	22
14	20	23
15	19	22
16	14	23
17	23	23
18	21	24
19	18	25
20	23	25
21	29	26
22	30	25
23	31	25
<b>TOTAL</b>	<b>481</b>	<b>568</b>

**Appendix 2. Summary of the best model (M3) for table 4 and used in figure 3.**

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)

['glmerMod']

Family: binomial ( logit )

Formula: Prey ~ 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)) + (1 | ID)

Data: visits

AIC	BIC	logLik	deviance	df.resid
773.3	808.1	-378.7	757.3	560

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.5636	-1.1186	0.7039	0.8431	1.2663

Random effects:

Groups Name	Variance	Std.Dev.
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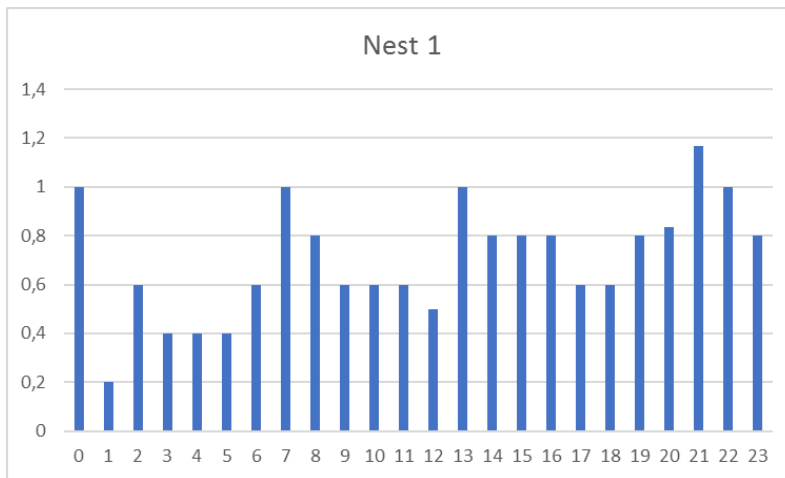
ID (Intercept)	0.02013	0.1419
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Number of obs: 568, groups: ID, 3

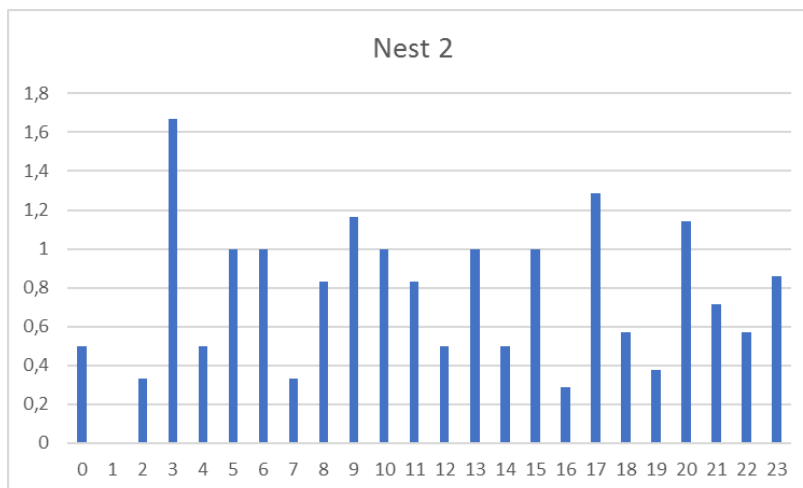
Explanatory values	Estimate	SE	Z	P
(Intercept)	0.3000	0.1238	2.424	0.0154
I(cos(2 * pi * Hour/24))	-0.1121	0.1215	-0.923	0.3559
I(sin(2 * pi * Hour/24))	-0.1006	0.1230	-0.818	0.4137
I(cos(2 * 2 * pi * Hour/24))	-0.2090	0.1224	-1.708	0.0877
I(sin(2 * 2 * pi * Hour/24))	-0.1301	0.1221	-1.065	0.2868
I(cos(3 * 2 * pi * Hour/24))	-0.1725	0.1218	-1.417	0.1566
I(sin(3 * 2 * pi * Hour/24))	-0.3105	0.1226	-2.533	0.0113

**Appendix 3a-c. The rate of prey deliveries to the hawk owl nests per hour-block.**

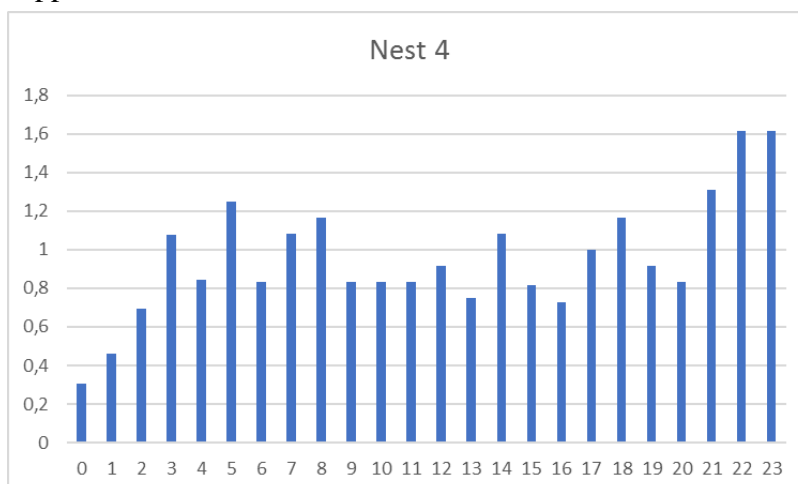
Appendix 3a



Appendix 3b



Appendix 3c





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