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## **Diet and diel pattern in the tawny owl (*Strix aluco*)**

Diett og døgnaktivitet hos kattugle  
(*Strix aluco*)

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Teacher Education in Natural Sciences



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# Abstract

Through continuous video monitoring of three tawny owls (*Strix aluco*) nests in Akershus county in southeast Norway during April and May 2016. I recorded prey deliveries and prey handling. A total of 284 prey items were registered, adding up to a total of 6795.7 g of prey mass delivered with a mean prey mass of 24.4 g. The prey mass ranged from 0.2-300 g. All prey items were identified to species or higher taxa. Vertebrates accounted for 89.4 % of all prey items by number and 99.2 % by mass, invertebrates accounted for 9.9 % by number and 0.1 % by mass, while unidentified prey accounted for 0.7 % by number and 0.7 % by mass. Mammals were the largest prey group accounting for 69.4 % by number and 78.0 % by mass, and within mammals, wood mouse (*Apodemus sylvaticus*) contributed the most with 31.0 % by number and 32.4 % by mass. Birds were the other large group accounting for 16.5 % by number and 17.2 % by mass. Other prey deliveries were amphibians (2.8 % by number and 3.0 % by mass) and reptiles (0.7 % by number and 1.0 % by mass). Most of the prey deliveries occurred during the night, and the highest probability (0.38) for a prey delivery happened during the hour block lasting from 22.00 to 22.59. The nestling's need for assistant feeding increased with prey mass and decreased as the nestlings grew older. The probability that mammals were ingested unassisted at least 50 % of the time occurred after 21 days and after 25 days for birds. The probability that any prey item was ingested unassisted at least 50 % of the time occurred after 20 days. The prey mass consumed per nestling increased with nestling age in a non-linear model and peaked at 24 days, while the prey mass consumed per nestling increased with the season (days after monitoring started at the first nest) in a linear model.

# Sammendrag

Ved kontinuerlig videoobservasjon på tre reir av kattugle (*Strix aluco*) i Akershus fylke i Sørøst-Norge i april og mai 2016, registrerte jeg byttedyrleveringer og byttedyrhåndtering. Totalt ble 284 bytter registrert, noe som gav 6795.7 g levert byttedyrmasse med en gjennomsnittsvekt på 24.4 g. Vekten på byttedyrene varierte fra 0.2-300 g. Alle byttedyr ble identifisert ned til art eller høyere klassifisering. Vertebrater utgjorde 89.4 % av alle byttedyrene i antall og 99.2 % i vekt, evertebrater utgjorde 9.9 % av alle byttedyrene i antall og 0.1 % i vekt, mens uidentifiserte byttedyr utgjorde 0.7 % av alle byttedyrene i antall og 0.7 % i vekt. Pattedyr var den største gruppen av byttedyr med 69.4 % av alle byttedyrene i antall og 78.0 % i vekt, og av pattedyr så var den vanligste arten skogmus (*Apodemus sylvaticus*) som stod for 31.0 % av antall byttedyr og utgjorde 32.4 % av total byttedyrmasse. Fugler var den andre store gruppa, og denne utgjorde 16.5 % av antall byttedyr og 17.2 % av total byttedyrmasse. Andre byttedyr som ble levert var amfibier (2.8 % i antall og 3.0 % i masse) og reptiler (0.7 % i antall og 1.0 % i masse). De fleste byttedyrleveringene forekom i løpet av natten, og den høyeste sannsynligheten (0.38) for at det forekom en byttedyrlevering var i timesblokken fra 22.00 til 22.59. Ungenes behov for fôringshjelp økte med byttedyrmasse og minket med ungens alder. Sannsynligheten for at et pattedyr ble spist uten hjelp i minst 50 % av gangene forekom etter 21 dager og for fugler etter 25 dager. Sannsynligheten for at et hvilket som helst byttedyr ble spist uten hjelp i minst 50 % av gangene forkom etter 20 dager. Byttedyrmasse konsumert per unge økte med ungenes alder i den ikke-lineære modellen og hadde en maksimumsverdi ved 24 dager, mens byttedyrmasse konsumert per unge økte med sesong (dvs. antall dager som hadde gått etter at videoobservasjonsperioden hadde startet) i den lineære modellen

# Table of contents

Acknowledgements .....	i
Abstract .....	ii
Sammendrag .....	iii
1. Introduction .....	2
2. Methods .....	4
2.1 Study area and species .....	4
2.2 Video monitoring.....	5
2.3 Video analysis.....	5
2.4 Estimation of prey body mass .....	6
2.5 Statistical analysis.....	7
3. Results .....	9
3.1 Diet composition.....	9
3.2 Diel distribution of prey deliveries regarding time of day .....	12
3.3 Prey handling in the nest .....	16
3.4 Consumed prey mass per nestling per day .....	21
4. Discussion .....	25
4.1 Diet composition.....	25
4.2 Diel distribution of prey deliveries regarding time of day .....	26
4.3 Prey handling in the nest .....	28
4.4 Consumed prey mass per nestling per day .....	30
5. Conclusion.....	31
6. References .....	32
Appendix .....	38

# 1. Introduction

Nestlings of raptors (i.e. falcons (Falconiformes), hawks (Accipitriformes) and owls (Strigiformes)) are dependent of parents for food in the first weeks of their life (Sonerud et al. 2014a). Raptors have a long period of pre- and post-fledging parental care compared to most other birds (Newton 1979). The adult female assist the newly hatched nestlings by providing warmth and protection, and the parents are the only providers of food until fledging (Newton 1979). After the nestlings have fledged, the parents continue providing food until the offspring are capable of hunting themselves (Newton 1979). The diet of raptors has mainly been investigated through analysis of pellets and other remains found at nest sites (Cramp 1985; Slagsvold et al. 2010). Through analysing pellets and remains the result might give a biased estimate of the raptors diet, overestimating birds and large prey items and underestimating mammals and small prey (Simmons et al. 1991; Slagsvold et al. 2010).

The most common mating pattern found in birds are social monogamy, and raptors are no exception (Ketterson & Nolan 1994; Gross 2005). The male and female share the burden of raising the offspring, but they have asymmetrical parental roles (Sonerud et al. 2013). During the first part of the nestling period, the male usually is the one hunting while the female take care of the nestlings (Eldegard & Sonerud 2010; 2012). Later in the nestling period the nestlings will need less assistance and then the female will start assisting the male in food gathering (Sonerud et al. 2014a). Prey preparation varies among different kind of prey types and prey species, and the timing of when the female starts hunting seems to vary with prey types (Sonerud et al. 2014b).

The tawny owl (*Strix aluco*) is a territorial, resident, medium sized and chiefly nocturnal owl that occurs throughout the Palearctic region (Cramp 1985; Jedrzejewski et al. 1996). It is found in a wide range of different habitats, including farmland, urban areas and forest areas (Cramp 1985; Hirons 1985; Obuch 2011). During hunting, the tawny owl mainly uses the sit-and-wait tactic stationed on a look-out post, but it can hunt in flight as well (Redpath 1995). The tawny owl uses both beak and claws to capture their prey (Cramp 1985). During the breeding season, tawny owls has been shown to have a home range of 1-2 km<sup>2</sup> in south-eastern Norway (Eldegard 1996). The tawny owls will use tree cavities, nest boxes and other

suitable cavities for nesting sites when available (Cramp 1985). With a diet including small mammals, birds, amphibians, insects and earthworms, the tawny owl is considered a food generalist (Cramp 1985). This will make the tawny owl highly adaptable to natural fluctuations in density of its prey species, even though the populations of tawny owl is reported to vary according to availability of small mammals (Karell et al. 2009).

Knowledge about the choice and handling of prey by the tawny owl is mainly based on studies of owl pellets (e.g. Jędrzejewski et al. 1994; Petty 1999), from dissection of prey remains (e.g. Balčiauskienė 2005; Balčiauskienė et al. 2005), and field observations (e.g. Southern 1969; Solonen 2009). These methods have been found to give inaccurate results (Errington 1930; 1932; Redpath et al. 2001). In the latter years, a new method to widen our knowledge about the choice and handling of prey by birds have arisen, video monitoring. As Lewis et al. (2004) show, video monitoring of prey deliveries give a more accurate estimate. By using video monitoring it is possible to monitor raptor nests continuously during day and night, which then in addition to choice and handling of prey will give valuable information about activity periods. Using video monitoring to study prey deliveries in raptors has become more common lately (e.g. Slagsvold et al. 2010; Sonerud et al. 2014a).

The main goal with my study was to gain accurate estimates of the diet and diel pattern of tawny owls, through video monitoring of three nest boxes from hatching until fledging. The information obtained was used to i) specify prey items delivered at the nest box; ii) register at what time the owls were active; iii) investigate what makes the parents assist the nestlings in feeding rather than let the nestlings feed by themselves; iv) investigate the differences on how long the nestlings need assisted feeding for different kind of prey types and; v) estimate the daily amount of prey mass delivered to the nestlings.



## 2. Methods

### 2.1 Study area and species

This study was performed in Akershus county in south-eastern Norway, within 12 km from the town of Ås (59°40'N, 10°47'E) during the spring of 2016. The three selected nest boxes were confirmed hosting tawny owl pairs before video recordings started. The three nest boxes were located in Hauger, Norderås and Jeksrud (Figure 1) and they were all mounted in large trees. At the location in Hauger the nest box had deciduous forest to the north, agricultural land to the south and mixed forests to the west and east. The nest box in Jeksrud had agricultural land to the west, and a large area of coniferous forest to the east. In Norderås the nest box was located in a small patch of deciduous forest which was surrounded by agricultural land to the south and west and mixed forest to the north and east.



**Figure 1:** The location of the three nest boxes used in this study, termed by the name of the locality (Norderås, Jeksrud and Hauger)

## **2.2 Video monitoring**

To monitor the nests I used a modification of the design described by Steen (2009). A camera was attached to wall right below the lid of each nest box, with a wide angle lens to cover the entrance hole and most of the area inside (Appendix 1). At all locations, I used a mini charged-coupled device (CCD) camera with infrared light to make it able to record in poor light conditions, i.e. during night. The camera was connected to a mini digital video recorder (DVR) that was hid on the ground together with a 12 V 80AH or 12 V 60AH battery. This was to avoid disturbing the tawny owls during change of battery and SD memory cards. Batteries and SD cards were changed every 5-7 days throughout the observation period. The mini DVRs that were used was Secumate H.264 Mini Portable DVRs. All recordings were saved on 32 GB SD cards. To avoid continuous recordings, all cameras had video motion detection (VMD), which makes it possible to trigger a recording only when there are some moving objects within the fixed field of the camera. To minimize recordings of nestlings moving, and only have recordings of parents leaving or arriving the nest box (see Steen (2009) for detailed description), the entire nest box except the entrance was digitally masked. Each recording had a 5s pre-recording before the trigger event occurred and a 10s post-recording after the trigger event ended. This pre-recordings and post-recordings made sure no valuable video evidence about prey deliveries was lost.

## **2.3 Video analysis**

A total of 83 hours and 37 minutes of recordings were made during the observation period. There was a total of 13660 video files and 288 contained prey deliveries. The recordings varied in length from 15-378s (6min and 18s). All recordings were assessed and those recordings containing prey delivery were carefully analysed. These recordings were analysed by myself together with Geir A. Sonerud and Vidar Selås more carefully to identify the prey delivered. To identify the prey items, body size, colouration, fur structure, head shape, ear size, tail length, length and colouration of the hind foot, eye size, beak shape and size, plumage, tarsus and overall appearance are used. For the prey items that were impossible to identify species, the identification stopped at some higher taxa (genus or family). Some prey items were impossible to identify more than to a bird, a mammal, an amphibian, a reptile or an insect.

I have chosen not to specify frogs (*Rana sp.*) or leaf warblers (*Phylloscopus sp.*) to species level. Frogs were assumed to be common frogs (*Rana temporaria*) mainly, but it was impossible to rule out the possibility that some of them might have been moor frogs (*Rana arvalis*). Leaf warblers were assumed to be willow warbler (*Phylloscopus trochilus*) mainly, but it was impossible to rule out the possibility that some of them were the common chiffchaff (*Phylloscopus collybita*). Every prey identified as *Apodemus sp.* were scored as wood mouse (*Apodemus sylvaticus*), because this is the only species of *Apodemus* that have been registered through a snap trapping program at Ås during spring from 1993 to 2016 (Geir A. Sonerud, pers. comm.)

To achieve the date and time of every prey delivery at the nest box, the exact time of when the owl landed at the entrance of the box were registered by viewing the time stamp on the video clip. Other parameters that were registered was nest ID, feeder (if the female fed her nestlings or if the nestlings fed by themselves), if the prey item were decapitated prior to delivery, if the prey were eaten at prior to delivery and which parent that delivered the prey. In addition to these parameters it was investigated when the female departed from the nest before she returned. The nestlings age was registered as the youngest nestling in each brood alongside the parameters temperature and precipitation.

The bird that delivered the prey item, was scored as female if the bird entered the nest box to interact with the nestlings, and as the male if it just dumped the prey item into the nest box or gave it to the other bird that were already inside the nest box.

## **2.4 Estimation of prey body mass**

Data from snap trapping at Ås from 1993 to 2016, were used to estimate the prey body mass of mammalian prey (Geir A. Sonerud, pers. comm.). The estimation of prey body mass for avian prey were taken as a mean value for each prey species from data adequate to the breeding season in Fennoscandia, because bird body mass has a relatively small intraspecific variation (Cramp 1988; Cramp 1992; Cramp & Perrins 1993; Cramp & Perrins 1994; Selås 2001). Passerines had the same mass assigned for adults and juveniles. The body mass of unidentified *Phylloscopus* species was taken from Sand (2016). Unidentified birds were given

an estimated prey mass based on the average prey mass of all birds that had a known prey mass. Reptiles and amphibians were given a body mass with the same procedure as for mammals (Vidar Selås, pers. comm.). The body mass of earthworms was taken by Stave (2015). Insect prey body mass was taken from Itämies and Korpimäki (1987). The prey mass of unidentified prey items, was taken as the average body mass for all the identified prey items in that nest.

## **2.5 Statistical analysis**

The statistical analysis was done using the software programs R version 3.3.3 (R Development Core Team 2014). In R version 3.3.3, the packages “lme4” (Bates et al. 2014) and “nlme” (Pinheiro et al. 2007) were used to conduct mixed-effect regression models. Logistic and linear regression models were used. Initially JMP Pro version 13.0.0 were used to get an overview of the data and to remove errors like typos and duplicates (SAS Institute Inc. 2015). Figures 2-4 and all tables were constructed using R, while figures 5-10 were constructed using SigmaPlot version 11.0 (Systat Software Inc. 2008).

The periodic components of time series were set as sine and cosine functions to analyse the circadian rhythm of the tawny owl (Pita et al. 2011). The sample unit was each hour of the day, i.e. the day was divided into 24 hour blocks, from 0 to 23 for each 24-hour period, and this was termed  $x$  in the models. The probability for a prey to be delivered in a certain hour block was set to be the response variable. If there were one or more prey deliveries within an hour block, it was scored as “yes”, if there were no prey deliveries within an hour block, it was scored as “no”, which makes this a conservative test. The random effect was a correction for the nest ID, and was called  $\epsilon$  in the models. All models were sorted by AIC values (Burnham & Anderson 2002). The models ( $M_1$ - $M_4$ ) were as follows:

$$M_1: \text{logit}(f(x)) = a_0 + \varepsilon$$

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

$$M_3: \text{logit}(F(x)) = a_0 + \left( a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left( a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_{21} \sin \frac{2 \cdot 2\pi x}{24} \right) + \varepsilon$$

$$M_4: \text{logit}(F(x)) = a_0 + \left( a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left( a_2 \cos \frac{2 \cdot 2\pi x}{24} + b_2 \sin \frac{2 \cdot 2\pi x}{24} \right) + \left( a_3 \cos \frac{3 \cdot 2\pi x}{24} + b_3 \sin \frac{3 \cdot 2\pi x}{24} \right) + \varepsilon$$

Further, a test was done for the probability that the female would assist feeding rather than the nestlings would ingest a prey item unassisted, with prey mass (g) and nestling age (d) as explanatory variables. Another switch test for the probability that the prey item ingested unassisted was done for mammals and birds separately, with nestling age (d) as explanatory variable. Finally, the prey mass consumed per nestling per day (24 h) was tested, with prey mass (g) as the response variable, and both nestling age (d) and season (i.e. number of days after 22 April, when the video monitoring period started) as the explanatory variables in two different tests. The non-linear model was chosen as the model for nestling age with response variable based on AIC values (Burnham & Anderson 2002). As for the model with season as a response variable both models were chosen as their AIC values were similar, even though  $\Delta\text{AIC}$  were  $>2.00$  (Burnham & Anderson 2002). In the analysis of prey mass consumed per nestling per day (24 h) only days before any nestlings fledged were used, making this a conservative test. Nest ID was included as a random effect in all tests and estimates.

## 3. Results

### 3.1 Diet composition

The diet of the tawny owls consisted of a wide variety of prey species (Table 1). In total, 284 prey items were recorded at the three tawny owl nests. The 284 prey items consisted of 28 species, where 7 species of mammals and 12 species of birds (Table 1). Identified vertebrates accounted for 89.4 % of all prey items, while invertebrates accounted for 9.9 %. The remaining 0.7 % of prey items were unidentified. Within vertebrates, mammals were the largest group of prey by numbers (69.4 %), followed by birds (16.7 %), amphibians (2.8 %) and reptiles (0.7 %) (Table 1). Among mammals, wood mouse was the most numerous prey species, accounting for 31.0 % by number. Field vole (13.0 %) and common shrew (11.6 %) were the second and third most numerous prey items (Table 1). In terms of prey mass, mammals were the largest group accounting for 78.0 % of the total prey mass delivered, followed by birds (17.2 %), amphibians (3.0 %), reptiles (1.0 %), invertebrates (0.2 %), and unidentified prey items (0.7 %) (Table 2). Among mammals, wood mouse contributed the most in terms of prey mass (32.4 %), followed by field vole (17.4 %) and Norway rat (7.4 %) (Table 2). The average prey body mass was 24.4 g (corrected for nest ID), but the prey body mass ranged from 0.2-300 g.

**Table 1:** Number of prey items recorded at the three tawny owl nests monitored by video during the breeding season 2016. The three nests are denoted by their locality name.

Species	Hauger		Norderås		Jeksrud		Total	
	No.	%	No.	%	No.	%	No.	%
Bank vole ( <i>Myodes glareous</i> )	7	6.5	3	3.8	4	4.2	14	4.9
Common shrew ( <i>Sorex araneus</i> )	13	12.0	6	7.5	14	14.6	33	11.6
Field vole ( <i>Microtus agrestis</i> )	7	6.5	9	11.3	21	21.9	37	13.0
Norway rat ( <i>Rattus norvegicus</i> )	0	0.0	2	2.5	0	0.0	2	0.7
Eurasian water shrew ( <i>Neomys fodiens</i> )	2	1.9	0	0.0	0	0.0	2	0.7
European water vole ( <i>Arvicola amphibius</i> )	0	0.0	3	3.8	0	0.0	3	1.1
Wood mouse ( <i>Apodemus sylvaticus</i> )	41	38.0	13	16.3	34	35.4	88	31.0
Unidentified small rodent	2	1.9	10	12.5	1	1.0	13	4.6
Unidentified small mammal	1	0.9	1	1.3	3	3.1	5	1.8
<b>Mammals total</b>	<b>73</b>	<b>67.6</b>	<b>47</b>	<b>58.8</b>	<b>77</b>	<b>80.2</b>	<b>197</b>	<b>69.4</b>
Coal tit ( <i>Periparus ater</i> )	0	0.0	0	0.0	1	1.0	1	0.4
Common chaffinch ( <i>Fringilla coelebs</i> )	0	0.0	1	1.3	0	0.0	1	0.4
Common redstart ( <i>Phoenicurus phoenicurus</i> )	0	0.0	0	0.0	1	1.0	1	0.4
European greenfinch ( <i>Chloris chloris</i> )	1	0.9	0	0.0	0	0.0	1	0.4
Great tit ( <i>Parus major</i> )	5	4.6	1	1.3	0	0.0	6	2.1
Western jackdaw ( <i>Corvus monedula</i> )	0	0.0	2	2.5	0	0.0	2	0.7
Unidentified thrush ( <i>Turdus</i> sp.)	1	0.9	0	0.0	1	1.0	2	0.7
Unidentified tit ( <i>Poecile</i> sp.)	3	2.8	0	0.0	0	0.0	3	1.1
Unidentified warbler ( <i>Phylloscopus</i> sp.)	1	0.9	0	0.0	0	0.0	1	0.4
Unidentified pipit ( <i>Anthus</i> sp.)	0	0.0	0	0.0	1	1.0	1	0.4
Unidentified tit (Paridae sp.)	1	0.9	0	0.0	1	1.0	2	0.7
Unidentified warbler (Sylviidae sp.)	2	1.9	0	0.0	2	2.1	4	1.4
Unidentified small bird	4	3.7	5	6.3	9	9.4	18	6.3
Unidentified bird	1	0.9	3	3.8	0	0.0	4	1.4
<b>Birds total</b>	<b>19</b>	<b>17.6</b>	<b>12</b>	<b>15.0</b>	<b>16</b>	<b>16.7</b>	<b>47</b>	<b>16.5</b>
Common toad ( <i>Bufo bufo</i> )	0	0.0	0	0.0	1	1.0	1	0.4
Frog ( <i>Rana</i> sp.)	1	0.9	4	5.0	2	2.1	7	2.5
<b>Amphibians total</b>	<b>1</b>	<b>0.9</b>	<b>4</b>	<b>5.0</b>	<b>3</b>	<b>3.1</b>	<b>8</b>	<b>2.8</b>
Grass snake ( <i>Natrix natrix</i> )	1	0.9	0	0.0	0	0.0	1	0.4
Slow worm ( <i>Anguis fragilis</i> )	1	0.9	0	0.0	0	0.0	1	0.4
<b>Reptiles total</b>	<b>2</b>	<b>1.9</b>	<b>0</b>	<b>0.0</b>	<b>0</b>	<b>0.0</b>	<b>2</b>	<b>0.7</b>
Earthworm ( <i>Lumbricidae</i> )	3	2.8	8	10.0	0	0.0	11	3.9
Unidentified beetle	0	0.0	2	2.5	0	0.0	2	0.7
Unidentified geometer moth	1	0.9	0	0.0	0	0.0	1	0.4
Unidentified owlet moth (Noctuidae)	9	8.3	1	1.3	0	0.0	10	3.5
Unidentified insect larvae	0	0.0	4	5.0	0	0.0	4	1.4
<b>Invertebrates total</b>	<b>13</b>	<b>12.0</b>	<b>15</b>	<b>18.8</b>	<b>0</b>	<b>0.0</b>	<b>28</b>	<b>9.9</b>
Unidentified prey	0	0.0	2	2.5	0	0.0	2	0.7
<b>Prey total</b>	<b>108</b>	<b>100.0</b>	<b>80</b>	<b>100.0</b>	<b>96</b>	<b>100.0</b>	<b>284</b>	<b>100.0</b>

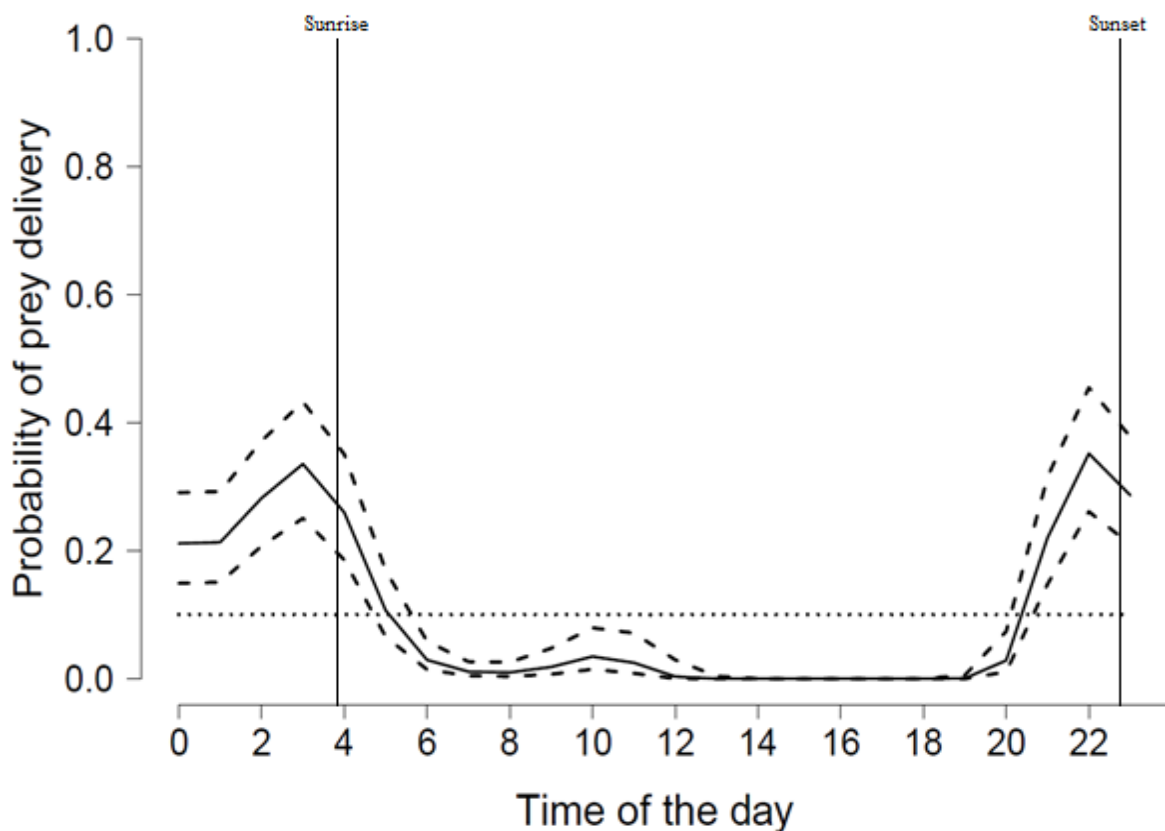
**Table 2:** Mass of prey items recorded delivered at the three tawny owl nests monitored by video during the breeding season 2016. The three nests are denoted by their locality name

Species	Hauger		Norderås		Jeksrud		Total	
	g	%	g	%	g	%	g	%
Bank vole ( <i>Myodes glareous</i> )	154	7.4	66	2.6	88	4.0	308	4.5
Common shrew ( <i>Sorex araneus</i> )	130	6.2	130	5.1	140	6.3	330	4.9
Eurasian water shrew ( <i>Neomys fodiens</i> )	30	1.4	0	0.0	0	0.0	30	0.4
European water vole ( <i>Arvicola amphibius</i> )	0	0.0	300	11.7	0	0.0	300	4.4
Field vole ( <i>Microtus agrestis</i> )	224	10.7	288	11.2	672	30.3	1184	17.4
Norway rat ( <i>Rattus norvegicus</i> )	0	0.0	500	19.5	0	0.0	500	7.4
Wood mouse ( <i>Apodemus sylvaticus</i> )	1025	49.0	325	12.6	850	38.3	2200	32.4
Unidentified small rodent	52	2.5	260	10.1	26	1.2	338	5.0
Unidentified small mammal	22	1.1	22	0.9	66	3.0	110	1.6
<b>Mammals total</b>	<b>1637</b>	<b>78.2</b>	<b>1891</b>	<b>73.6</b>	<b>1842</b>	<b>83.0</b>	<b>5300</b>	<b>78.0</b>
Coal tit ( <i>Pariparus ater</i> )	0	0.0	0	0.0	12	0.5	12	0.2
Common chaffinch ( <i>Fringilla coelebs</i> )	0	0.0	23	0.9	0	0.0	23	0.3
Common redstart ( <i>Phoenicurus phoenicurus</i> )	0	0.0	0	0.0	16	0.7	16	0.2
European greenfinch ( <i>Chloris chloris</i> )	27	1.3	0	0.0	0	0.0	27	0.4
Great tit ( <i>Parus major</i> )	90	4.3	18	0.7	0	0.0	108	1.6
Western jackdaw ( <i>Corvus monedula</i> )	0	0.0	312	12.1	0	0.0	312	4.6
Unidentified thrush ( <i>Turdus</i> sp.)	80	3.8	0	0.0	80	3.6	160	2.4
Unidentified tit ( <i>Poecile</i> sp.)	36	1.7	0	0.0	0	0.0	36	0.5
Unidentified warbler ( <i>Phylloscopus</i> sp.)	9	0.4	0	0.0	0	0.0	9	0.1
Unidentified pipit ( <i>Anthus</i> sp.)	0	0.0	0	0.0	21	0.9	21	0.3
Unidentified tit (Paridae sp.)	12	0.6	0	0.0	12	0.5	24	0.4
Unidentified warbler (Sylviidae sp.)	20	1.0	0	0.0	20	0.9	40	0.6
Unidentified small bird	60	2.9	75	2.9	135	6.1	270	4.0
Unidentified bird	27	1.3	81	3.2	0	0.0	108	1.6
<b>Birds total</b>	<b>361</b>	<b>17.3</b>	<b>509</b>	<b>19.8</b>	<b>296</b>	<b>13.3</b>	<b>1166</b>	<b>17.2</b>
Common toad ( <i>Bufo bufo</i> )	0	0.0	0	0.0	30	1.4	30	0.4
Frog ( <i>Rana</i> sp.)	25	1.2	100	3.9	50	2.3	175	2.6
<b>Amphibians total</b>	<b>25</b>	<b>1.2</b>	<b>100</b>	<b>3.9</b>	<b>80</b>	<b>3.6</b>	<b>205</b>	<b>3.0</b>
Grass snake ( <i>Natrix natrix</i> )	50	2.4	0	0.0	0	0.0	50	0.7
Slow worm ( <i>Anguis fragilis</i> )	15	0.7	0	0.0	0	0.0	15	0.3
<b>Reptiles total</b>	<b>65</b>	<b>3.1</b>	<b>0</b>	<b>0.0</b>	<b>0</b>	<b>0.0</b>	<b>65</b>	<b>1.0</b>
Earthworm ( <i>Lumbricidae</i> )	2.4	0.1	6.4	0.2	0	0.0	8.8	0.1
Unidentified beetle	0	0.0	0.4	0.0	0	0.0	0.4	0.0
Unidentified geometer moth	0.2	0.0	0	0.0	0	0.0	0.2	0.0
Unidentified owlet moth (Noctuidae)	1.8	0.1	0.2	0.0	0	0.0	2	0.0
Unidentified insect larvae	0	0.0	0.8	0.0	0	0.0	0.8	0.0
<b>Invertebrates total</b>	<b>4.4</b>	<b>0.2</b>	<b>7.8</b>	<b>0.3</b>	<b>0</b>	<b>0.0</b>	<b>12.2</b>	<b>0.1</b>
Unidentified prey	0.0	0.0	62.6	2.4	0.0	0.0	47.5	0.7
<b>Prey total</b>	<b>2092.4</b>	<b>100.0</b>	<b>2570.4</b>	<b>100.0</b>	<b>2218.0</b>	<b>100.0</b>	<b>6795.7</b>	<b>100.0</b>



### 3.2 Diel distribution of prey deliveries regarding time of day

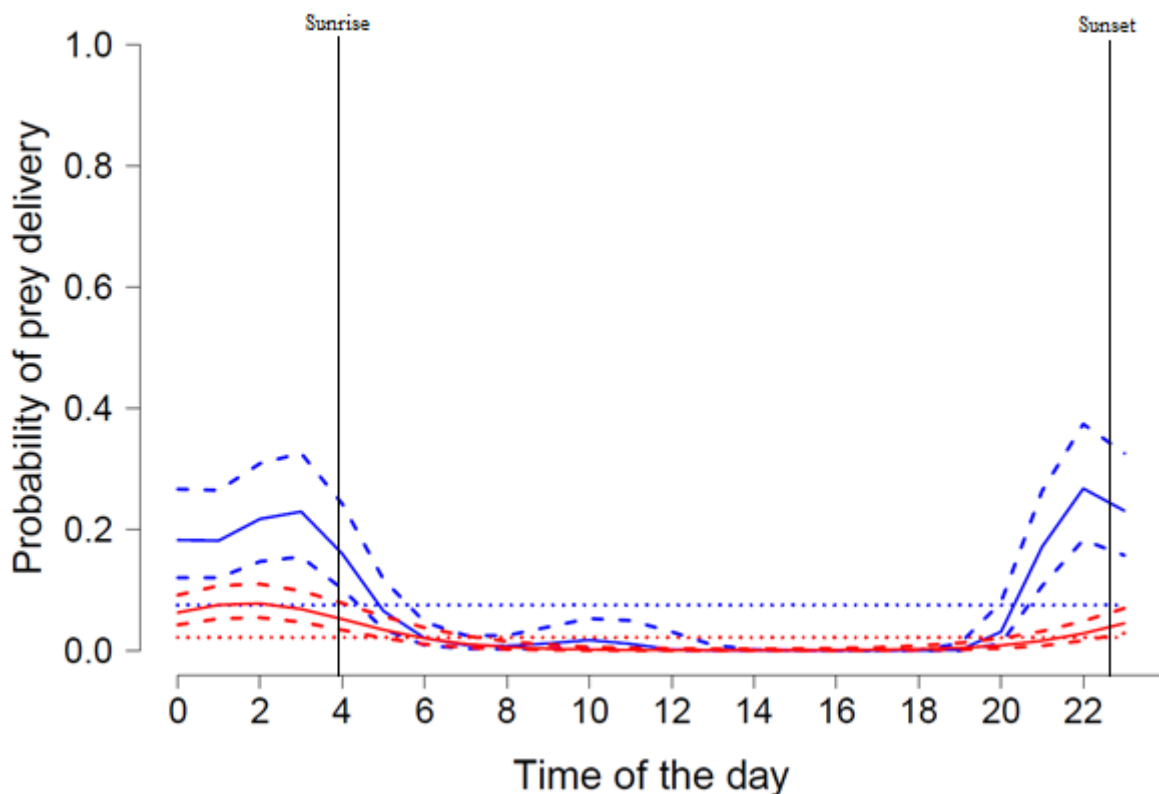
The probability of a prey delivery was in general low during day time and higher during the night (Figure 2, Appendix 2). In my study area, during the monitoring period sunrise occurred on average at 03.45 hour and sunset occurred on average at 22.45 hour. The probability of getting a prey delivery peaked at the hour block lasting from 03.00 to 03.59 with a value of 0.36. Another peak occurred in the hour block lasting from 22.00 to 22.59 with a value of 0.38, showing that the probability of a prey delivery was elevated around sunrise and sunset (Figure 2).



**Figure 2:** The probability of at least one prey delivery per hour block as a function of time of day (h) at the three tawny owl nests monitored, predicted by models of circadian activity rhythms. The dotted line is the midline estimating statistic of rhythm (MESOR). The two dashed lines denote the 95 % confidence interval. The vertical lines denote the average time of sunrise and sunset during the monitoring period.

The probability of delivery was higher for a mammalian prey than for an avian prey throughout the entire day (Figure 3, Appendices 3 and 4). The probability of delivery of a mammalian prey peaked at the hour block lasting from 03.00 to 03.59, with a value of 0.23, and at the hour block lasting from 22.00 to 22.59, with a value of 0.29. The corresponding

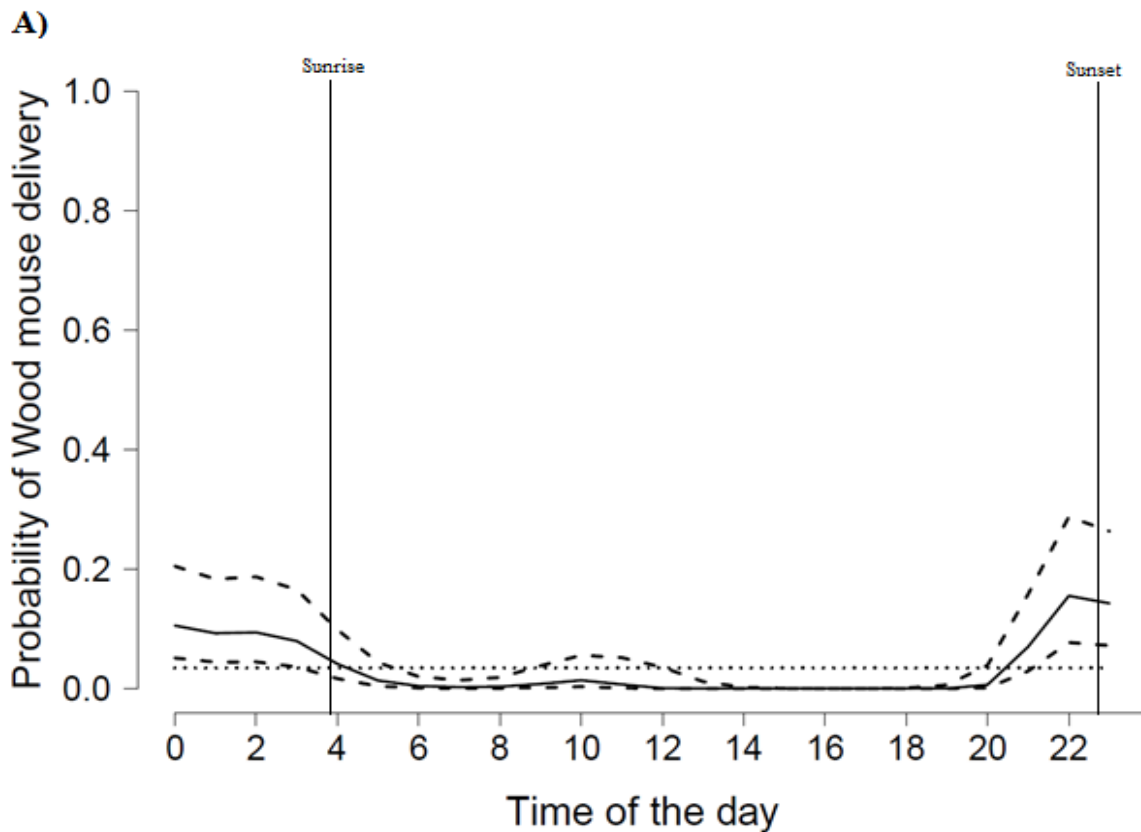
probability for an avian prey to be delivered peaked at the hour block lasting from 02.00 to 02.59, with a value of 0.08. The time at which the probability of a prey delivery became lower than average in the morning and higher than average in the evening (i.e. below and above the MESOR), occurred one hour later and earlier, respectively for mammalian prey than for avian prey (Figure 3).



**Figure 3:** The probability of at least one prey delivery per hour block as a function of time of day (h) at the three tawny owl nests monitored, predicted by models of circadian activity rhythms, for birds (red lines) and mammals (blue lines). The dotted line is the midline estimating statistic of rhythm (MESOR). The dashed lines denote the 95 % confidence interval. The vertical lines denote the average time of sunrise and sunset during the monitoring period.

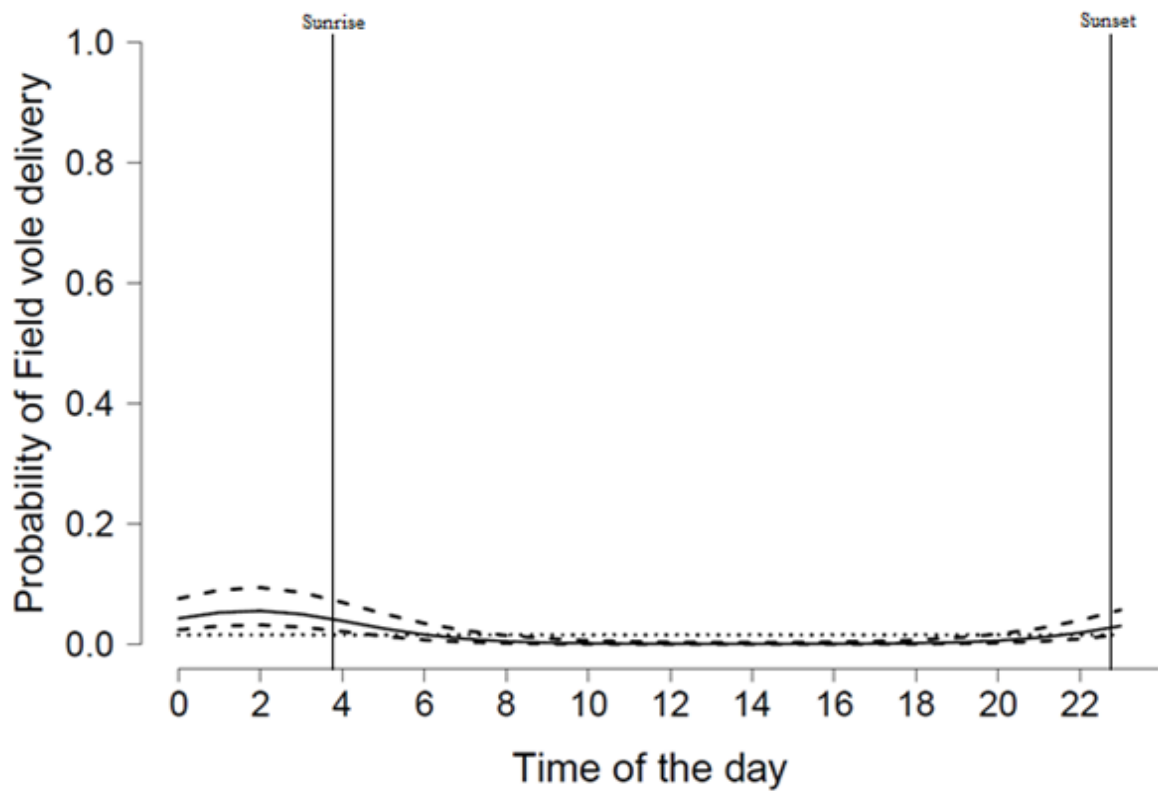
Within the mammalian prey group, the probability of at least one prey delivery peaked at the hour block lasting from 22.00 to 22.59 for wood mouse, with a value of 0.18 (Figure 4 A, Appendix 5). Within the hours 10.00 to 12.00, the tawny owl delivered three wood mice to the nest box at location Hauger (Figure 3, Figure 4 A). These deliveries occurred when the nestling age were 16 days old, 19 days old and 21 days old. For field vole, the probability of at least one prey delivery peaked at the hour block lasting from 02.00 to 02.59, with a value of

0.09 (Figure 4 B, Appendix 6). For common shrew, the probability of at least one prey delivery peaked at the hour block lasting from 00.00 to 00.59, with a value of 0.10 (Figure 4 C, Appendix 7).

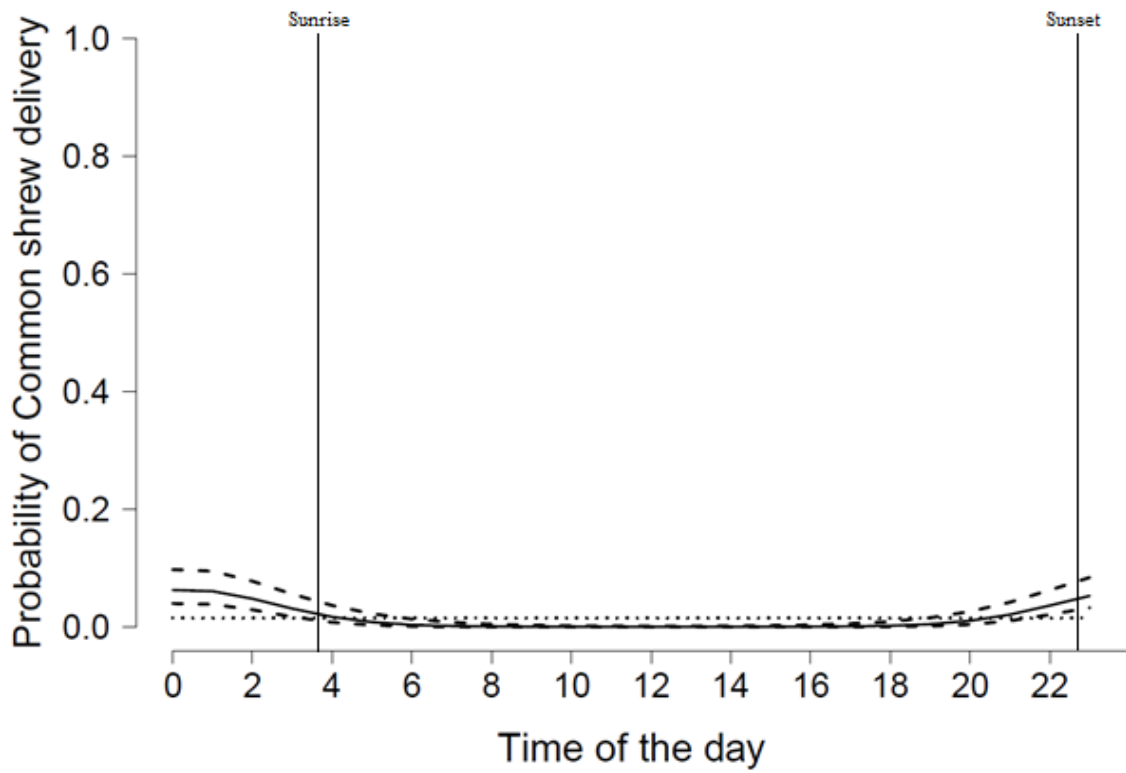


**Figure 4:** The probability of at least one prey delivery of wood mouse (A), field vole (B) and common shrew (C) per hour block as a function of time of day (h) at the three tawny owl nests video monitored, predicted by models of circadian activity rhythms. The dotted line is the midline estimating statistic of rhythm (MESOR). The dashed lines denote the 95 % confidence interval. The vertical lines denote the average time of sunrise and sunset during the monitoring period.

**B)**

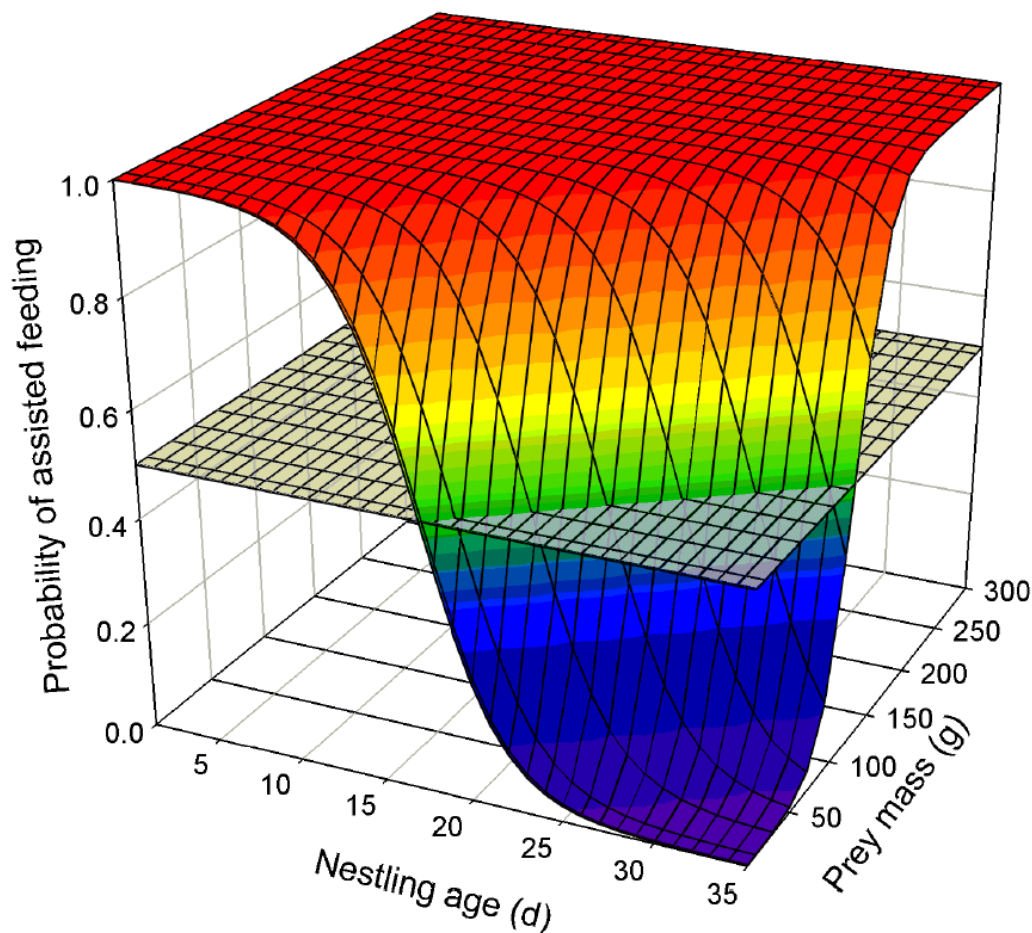


**C)**



### 3.3 Prey handling in the nest

A model that explained the probability for the female to assist in feeding as a function of prey mass and age of nestling as explanatory variables was constructed (Table 3). The tawny owl nestlings' need for assisted feeding decreased with their age, and increased with the body mass of the prey (Figure 5, Table 3). The female assisted the nestlings to feed on all the prey items delivered at the beginning of the monitoring period, but as the nestlings grew older the probability of feeding assisted started to decrease for smaller prey items. The lowest predicted probability for the nestlings being fed assisted was when high nestling age was combined with low prey body mass (Figure 5). For small prey items the probability of the nestlings being fed assisted was the same as for the nestling to feed unassisted after 17 days (Figure 5), while for large prey items the nestlings needed assistance at all times (Figure 5).

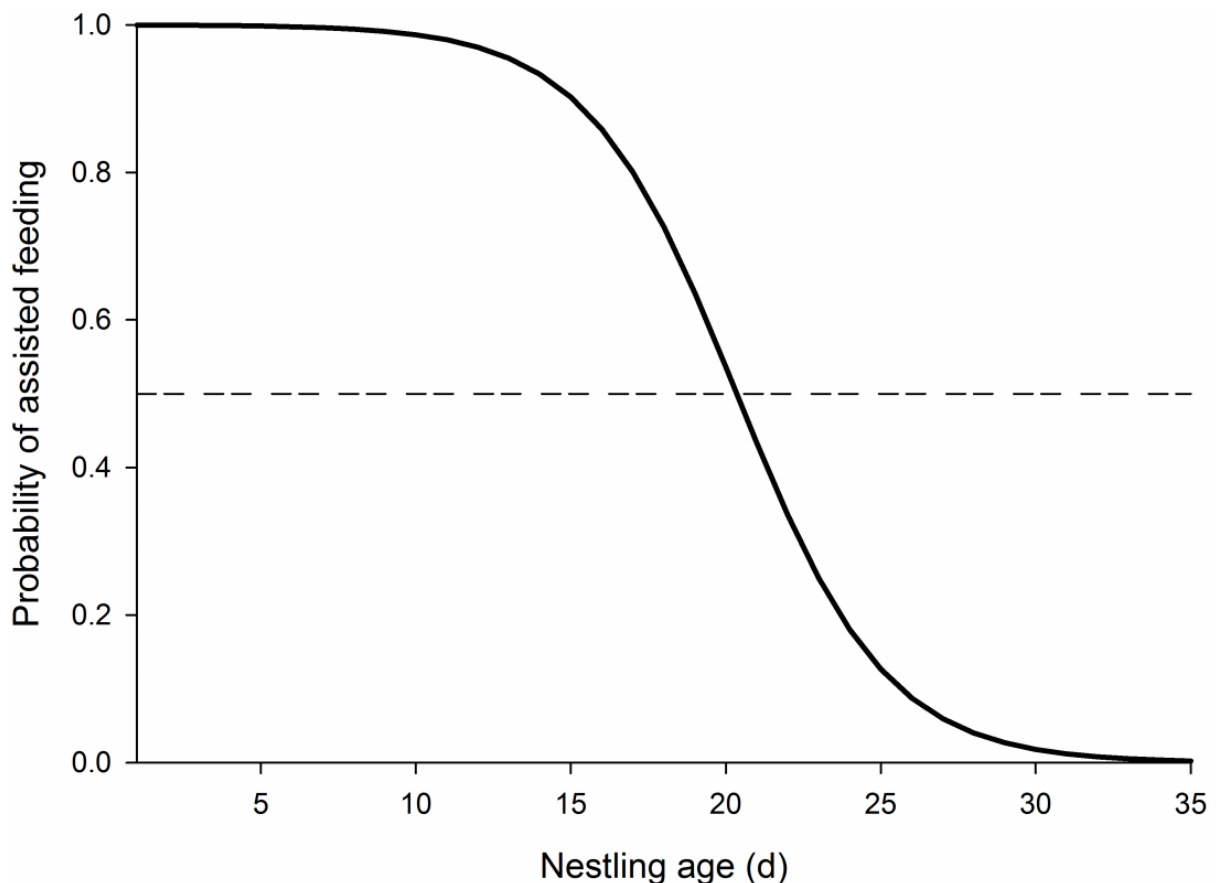


**Figure 5:** The probability that a tawny owl female assisted the nestlings in ingesting a prey item as a function of nestling age (d) and prey mass (g). The switch, when the probability for the female to assist the nestlings to ingest a prey item was the same as the probability for the nestlings to ingest the prey item unassisted, is shown with a horizontal transparent grid. Nestling age is classified as the youngest nestling in a brood.

**Table 3:** Parameter estimates from the model of the probability that a tawny owl female assisted the nestling in ingesting the prey item as a function of nestling age (d) and prey mass (g). The model is corrected for nest ID (n = 195, random effect = 3 nests).

	Estimates	SE	z	p
Intercept	7.76532	1.95801	3.966	<0.0001
Nestling age	-0.45135	0.08617	-5.238	<0.0001
Prey mass	0.06848	0.02165	3.163	0.0016

A model that explained the probability for the female to assist in feeding as a function of nestling age as explanatory variable was constructed (Table 4). The tawny owl nestlings' need for assisted feeding decreased with their age (Figure 6, Table 4). For any kind of prey item the probability of the nestlings being fed assisted was the same as for the nestling to feed unassisted after 20 days (Figure 6).

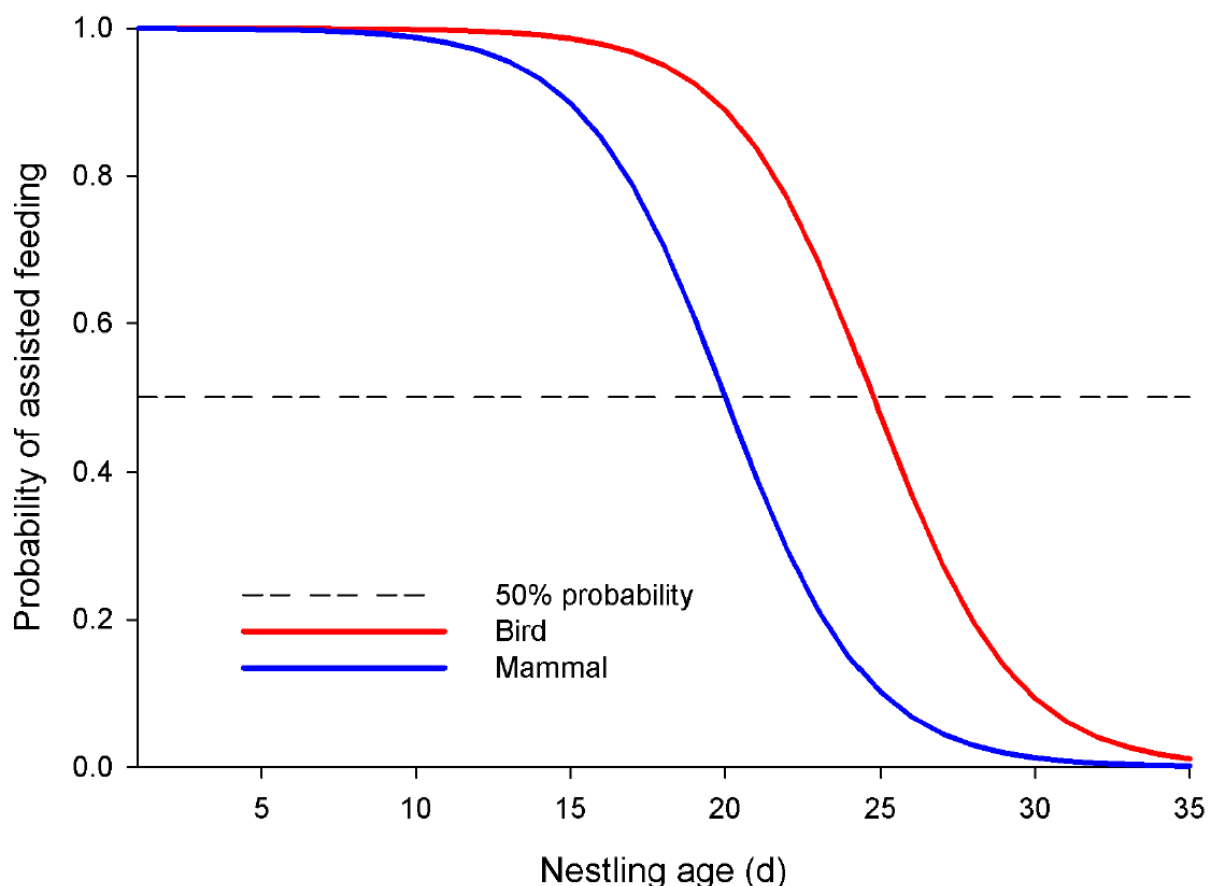


**Figure 6:** The probability that a tawny owl female assisted the nestlings in ingesting a prey item as a function of nestling age (d). The switch, when the probability for the female to assist the nestlings to ingest a prey item was the same as the probability for the nestlings to ingest the prey item unassisted, is shown with the stapled line. Nestling age is classified as the youngest nestling in a brood.

**Table 4:** Parameter estimates from the model of the probability that a tawny owl female assisted the nestling in ingesting the prey item as a function of nestling age (d). The model is corrected for nest ID (n = 195, random effect = 3 nests).

	Estimates	SE	z	p
Intercept	8.44438	1.91305	4.414	<0.0001
Nestling age	-0.41496	0.07801	-5.319	<0.0001

A model that explained the probability for the female to assist in feeding as a function of prey type (mammals vs. birds) and nestling age as explanatory variables was constructed (Table 5). The need for assisted feeding decreased with the nestlings age, but it decreased slower for birds than for mammals (Figure 7, Table 5). The estimated time at which the female had the same probability to assist feeding as the nestlings had to feed unassisted were 21 days for mammals and 25 days for birds (Figure 7).



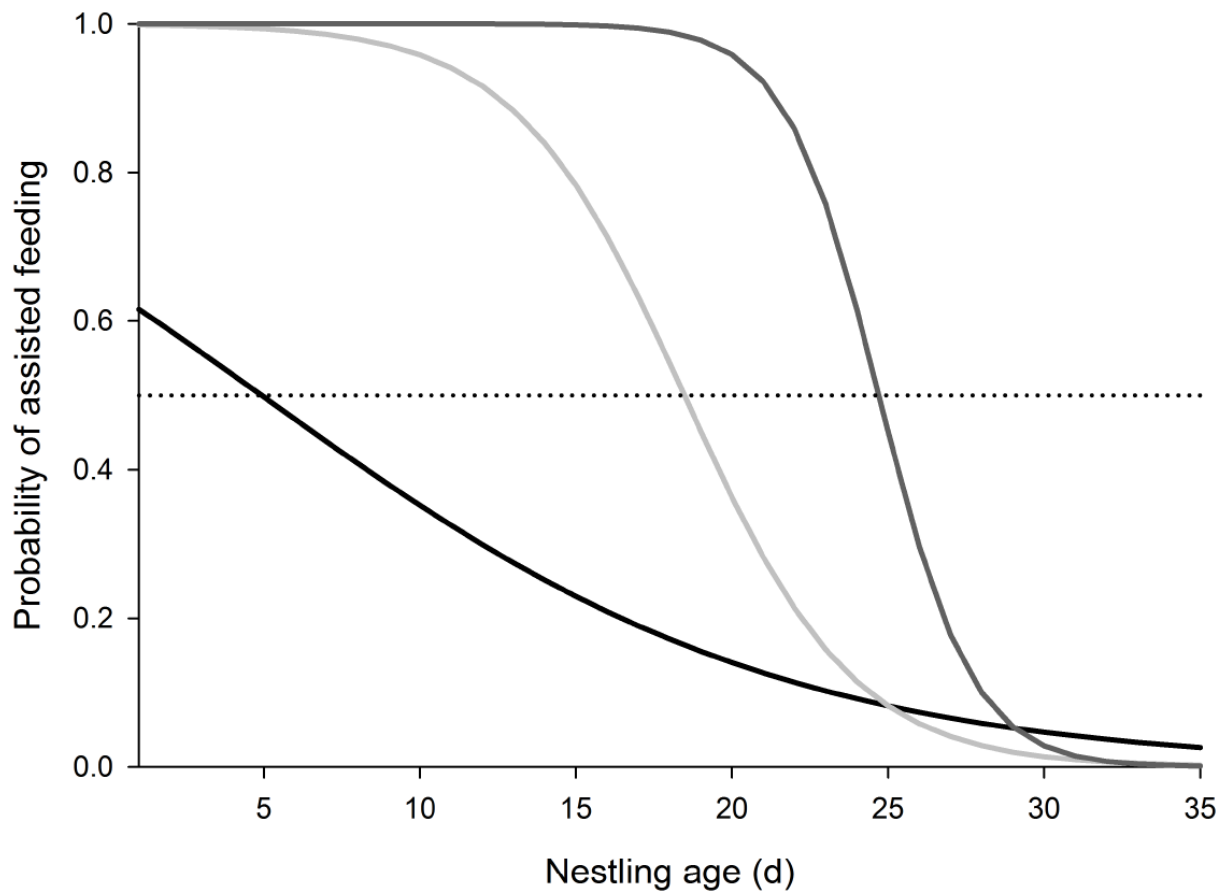
**Figure 7:** The probability that the tawny owl female assisted nestlings to ingest a prey item as a function of nestling age. Red line denotes avian prey, and blue line denotes mammalian prey. The switch, when the probability of the female assisting the nestlings in ingesting a prey item was the same as the probability of the nestlings ingesting the prey item unassisted, is shown with a dashed line. Nestling age is classified as the youngest nestling in a brood.

**Table 5:** Parameter estimates from the model showing the probability that a tawny owl nestling ingested the prey item without assistance as a function of nestling age (d) and if the prey were mammalian or avian. The model is corrected for nest ID (n = 162, random effect = 3 nests).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	10.80845	2.32156	4.656	<0.0001
Nestling age	-0.43625	0.08717	-5.005	<0.0001
Prey group, mammal or bird	-2.08040	0.76650	-2.714	0.0066

Three models that explained the probability of the female to assist in feeding as a function of nestling age, done separately at the three localities, as explanatory variables were constructed (Table 6). The tawny owl nestlings' need for assisted feeding decreased significantly with their age for locations Norderås and Jeksrud (Figure 8, Table 6 b, Table 6 c). The probability curve differed significantly between Hauger and Jeksrud (Figure 8, Table 6 a, Table 6 c). The estimated time at which the female had the same probability to assist feeding as the nestlings had to feed unassisted were when the nestlings was between 5 days at location Hauger, between 19 days at location Norderås, and between 25 days at location Jeksrud (Figure 8).





**Figure 8:** The probability that the tawny owl female assisted nestlings to ingest a prey item as a function of nestling age, nest ID and the interaction term. Black line denotes location Hauger, dark grey line denotes location Jeksrud and light grey line denotes location Norderås. The switch, when the probability of the female assisting the nestlings in ingesting a prey item was the same as the probability of the nestlings ingesting the prey item unassisted, is shown with a dotted line. Nestling age is classified as the youngest nestling in a brood.

**Table 6:** Parameter estimates from the model of the probability that a tawny owl female assisted the nestling in ingesting the prey item in locations; a) with Hauger as baseline (“dummy variable”), b) with Norderås as baseline (“dummy variable”), and c) Jeksrud as baseline (“dummy variable”), as a function of nestling age (d), nest ID and the interaction term. (n = 195)

a)	Estimates	SE	z	p
Intercept	0.5921	3.6550	0.162	0.87
Nestling age	-0.1202	0.1569	-0.766	0.44
Norderås vs Hauger	6.2394	4.4005	1.418	0.16
Jeksrud vs Hauger	15.8894	5.6240	2.825	0.0047
Nestling age: Norderås	-0.2496	0.1948	-1.281	0.20
Nestling age: Jeksrud	-0.5470	0.2352	-2.326	0.020

<b>b)</b>	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	6.8315	2.4506	2.788	0.0053
Nestling age	-0.3698	0.1156	-3.200	0.0014
Jeksrud vs Norderås	9.6500	4.9271	1.959	0.050
Hauger vs Norderås	-6.2394	0.4005	-1.418	0.16
Nestling age: Jeksrud	-0.2974	0.2099	-1.417	0.16
Nestling age: Hauger	0.2496	0.1948	1.281	0.20

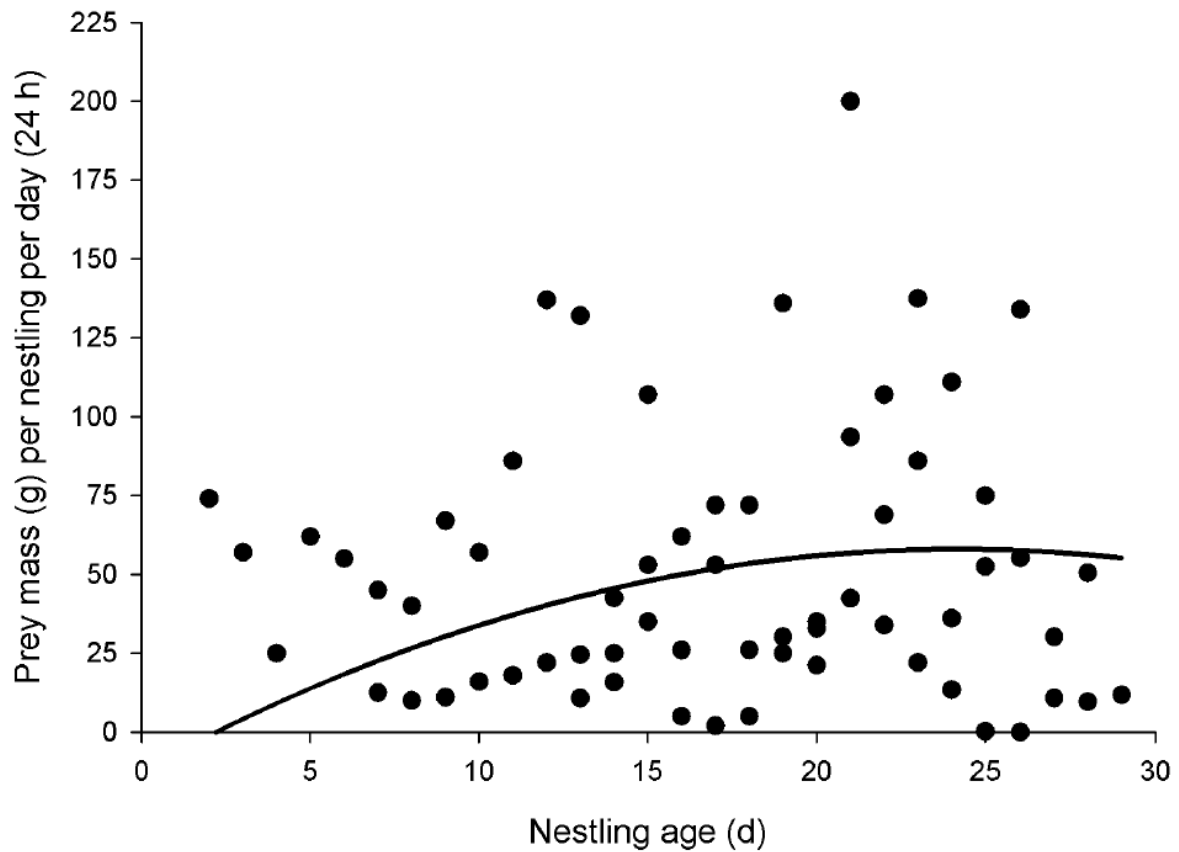
<b>c)</b>	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	16.4815	4.2744	3.856	0.0001
Nestling age	-0.6672	0.1753	-3.807	0.0001
Norderås vs Jeksrud	-9.6500	4.9271	-1.959	0.050
Hauger vs Jeksrud	-15.8894	5.6240	-2.825	0.0047
Nestling age: Norderås	0.2974	0.2099	1.417	0.16
Nestling age: Hauger	0.5470	0.2352	2.326	0.020

### 3.4 Consumed prey mass per nestling per day

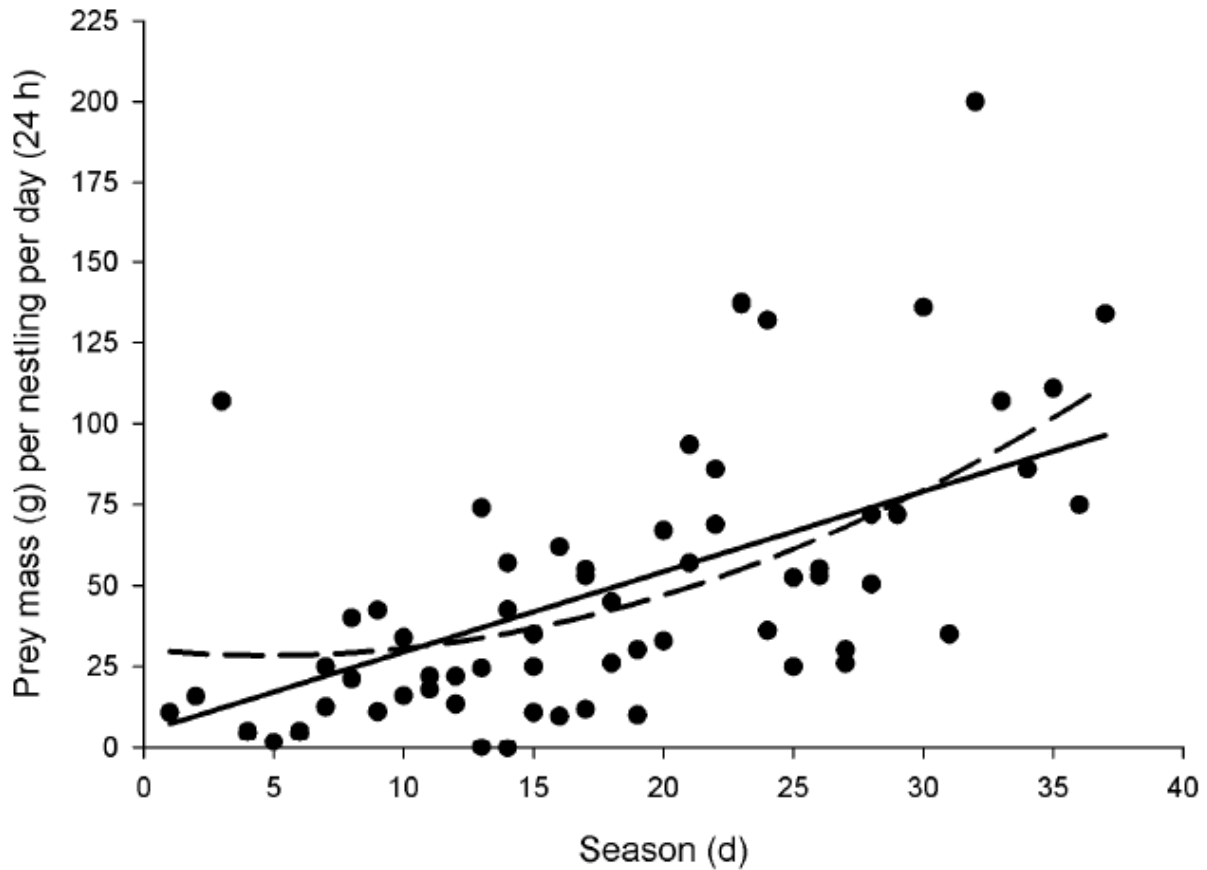
To describe prey mass consumed per nestling per day (24 h) three models were made. All models had prey mass consumed per nestling per day as a response variable. One of the two non-linear models had nestling age as an explanatory variable (Table 7), while the other non-linear model and the linear model had season (i.e. number of days after 22 April, when the video monitoring period started) as the explanatory variable (Table 8, Table 9). Of the two models having season as an explanatory variable, the best model was the linear model (Table 9), but the non-linear model ( $\Delta\text{AIC} = 3.5$ ) was included as it showed a trend (Figure 10, Table 8). Neither of the non-linear models was showing a significant relationship between gram per nestling per day (24 h) and nestling age or season (Table 7, Table 8), while the linear model showed a strong significance (Table 9).

As the nestlings grew older the estimated prey mass per day (24 h) that the nestlings consumed increased from 13 g at the age of 5 days, to peak at 59 g at 24 days, before it decreased to 51 g at 29 days (Figure 9). The linear model estimated that the prey mass per day

(24 h) that the nestlings consumed increased from 20 g after 5 days of monitoring to 92 g after 37 days of monitoring (Figure 10). The non-linear model estimated that the prey mass per day (24 h) that the nestlings consumed increased from 27 g after 5 days of monitoring to 111 g after 37 days of monitoring (Figure 10).



**Figure 9:** Non-linear model of prey mass (g) consumed per tawny owl nestling per day (24 h) as a function of nestling age (d).



**Figure 10:** A linear and a non-linear model of prey mass (g) consumed per tawny owl nestling per day (24 h) as a function of season (i.e. number of days after 22 April, when the video monitoring period started). Solid line denotes the best model, based on AIC values. Staped line denotes the non-linear model, showing a trend.

**Table 7:** Parameter estimates from the non-linear model showing the consumed prey mass (g) per nestling per day (24 h) as a function of nestling age (d). The model is corrected for nest ID ( $n = 64$ , random effect = 3 nests,  $AICc = 639.8$ ).

	Estimates	SE	t	p
Intercept	-12.201428	29.853132	-0.4087152	0.68
Age	5.808582	2.767223	2.0990656	0.040
I(Age <sup>2</sup> )	-0.120149	0.082606	-1.4544889	0.15

**Table 8:** Parameter estimates from the non-linear model showing the consumed prey mass (g) per nestling per day (24 h) as a function of season (d). The model is corrected for nest ID (n = 64, random effect = 3 nests, AICc = 636.2).

	<b>Estimates</b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	30.274178	18.660810	1.6223400	0.11
Season	-0.773808	1.942572	-0.3983418	0.69
I(Season <sup>2</sup> )	0.082569	0.047840	1.6841484	0.097

**Table 9:** Parameter estimates from the linear model showing the consumed prey mass (g) per nestling per day (24 h) as a function of season (d). The model is corrected for nest ID (n = 64, random effect = 3 nests, AICc = 632.7).

	<b>Estimates</b>	<b>SE</b>	<b>t</b>	<b>p</b>
Intercept	4.734767	11.494584	0.411913	0.68
Season	2.479556	0.543916	4.558710	<0.0001

## 4. Discussion

### 4.1 Diet composition

During the breeding season of 2016 the tawny owls had a broad diet. In total 284 prey items were delivered, it consisted of 28 species, where 7 species were mammalian and 12 species were avian. The prey items delivered to the tawny owl nestlings were by number, at least 69.4 % mammalian, at least 16.5 % avian, at least 2.8 % amphibian, at least 0.7 % reptilian, and at least 9.9 % invertebrates, while 0.7 % of the prey items could not be identified. By estimated prey body mass delivered, at least 78.0 % were mammalian, at least 17.2 % were avian, at least 3.0 % were amphibian, at least 1.0 % were reptilian, and at least 0.2 % were invertebrates, while 0.7 % was from prey items that could not be identified. Overall the wood mouse was the prey that was delivered the most, both in terms of number and biomass.

Rodents are most commonly reported to be the most numerous species in the tawny owls' diet, as well as counting for a substantial amount of the total prey mass consumed (e.g. Sunde et al. 2001; Solonen & Karhunen 2002; Zawadzka & Zawadzki 2007). The most frequently captured prey species seems to vary between years and areas (Balčiauskienė et al. 2005). In my study, wood mouse was the most numerous mammalian prey, followed by field vole and common shrew. The field vole is considered to be the main prey type of the tawny owl in most habitats (Millon et al. 2014). Therefore the high amount of wood mouse compared to field voles recorded in my study differ from results of previous research, but it coincide with Stave (2015) who got similar results in the same area as I used. Results from snap trapping in this area showed that 2016 had an all-time high in the wood mouse population in spring, and the second highest population recorded in fall (Geir A. Sonerud pers. comm). Taken this into account, it would be expected that the tawny owl would take a lot of wood mice, as the tawny owl adjusts its diet to the prey species found in its territory, and utilizes what is available in the given area (Cramp 1985).

The number of field voles found as prey in my study is an interesting observation, given that field voles mostly use open habitats (Corbet & Southern 1977), and that the tawny owl have been reported to avoid open habitats and prefer deciduous forests when hunting in my study area (Eldegard 1996). This finding fits with the indication that tawny owls did hunt on the

borders between forest and open areas that Sand (2016) found in her study from the same area. This indicates that the tawny owl would have been hunting outside of forest areas, and that it would have been hunting in more open areas, such as clear-cuts and fields or it may have been perching in the edge between forest and open areas. Shrews, bank voles and wood mice are most common in forests (Geir A. Sonerud pers. comm). This explains the high amount of shrews and wood mice, and it is in accordance with the preferred prey species in forests (Eldegard 1996). However, the bank voles did only account for 4.9 % of the total diet found in my study, which is lower than what both Stave (2015) and Sand (2016) found in their studies in the same area. Karell et al. (2009) suggested that the dynamics of the tawny owl is driven by the vole cycle, and that the tawny owl in Finland might show a numerical response to prey abundance. On the other hand, Petty (1999) found that in England the tawny owl responded functionally, rather than numerically, to vole abundance. Consider that the tawny owl is a food generalist, the diet of the tawny owl may reflect the available prey species in the given area. Other factors that could also be involved is, for instance, the individual hunting skills and preference, or the anti-predator defences in the prey species. For example, some rodents have been reported to reduce their overall activity, including foraging, as a response to having an owl in close presence (Eilam et al. 1999), which in turn might make them less available as a prey species for the owls. Other factors that may be the kind of vegetation type and the amount of ground cover in the area, which might affect how available the different prey species would be available as a prey for the owls (Southern 1954; Southern & Lowe 1968; Balčiauskienė 2005). As data on this was not gathered in my study, it is not possible to say if it had an effect here.

## **4.2 Diel distribution of prey deliveries regarding time of day**

Based on the probability of at least one prey delivery within an hour block, the tawny owls were mostly active and hunting during the night. They did most of their hunting around sunset and around sunrise, and showed a clear bimodal pattern. This fits well with the fact that the tawny owl is a nocturnal species (Cramp 1985). The probability of at least one prey delivery of any kind peaked at 0.38 between 22.00 and 22.59. In addition to this, some prey deliveries did occur at daytime, which have also been reported to occur during the breeding season of the tawny owl in previous studies (Cramp 1985; Stave 2015; Sand 2016). As nestlings grow their demand for food increases (Barba et al. 2009), which might explain why some prey deliveries were during daytime and why they happened later in the nestling period.

Overall, mammals had a higher probability of being delivered within an hour block during the activity period of the owls compared to the probability of an avian prey delivery. Wood mouse is often referred to as a monophasic species (e.g. Greenwood 1978; Flowerdew 2000), i.e. the activity pattern is one long activity phase. As the wood mouse is nocturnal (e.g. Greenwood 1978; Flowerdew 2000), the wood mouse's activity phase occurs during night time. This makes the wood mouse available as a prey species for the tawny owl during night. But as shown in my study some wood mouse, enough to elevate the predicted probability, was delivered during day time. This contradicts what was found by Greenwood (1978) and Flowerdew (2000), that the wood mouse is monophasic. Microtines and shrews show a distinct polyphasic activity pattern (e.g. Davis 1933; Brown 1956; Merritt & Vessey 2000; Halle & Stenseth 2012), i.e. a short-termed rhythm in activity that switches between rest and active phases during day and night. This would explain why the tawny owl could deliver them throughout the night, but it would be expected that some deliveries could happen during the day as well.

The probability of at least one avian prey delivery per hour block were higher during the night than during the day, but it was still a lower probability than for mammals. Out of 47 avian prey deliveries, only three were delivered between 06.00 and 21.00. One of those three prey deliveries were even delivered at 06.06, quite close to the hours chosen to represent daylight. This clearly show that the availability of avian prey must have been quite high during the night. In my study the birds accounted for 16.5 % of the diet, which is closely the same amount that Stave (2015), birds accounted for 18.3 % of total prey delivered, and Sand (2016), birds accounted for 15.0 % of total prey delivered, found in their studies. The “sit-and-wait” tactic is the most common hunting method among tawny owls, but they are capable of adjusting hunting method to the available prey type (Cramp 1985). When hunting for avian prey, tawny owls are known to catch roosting birds (Harrison 1960), and will use methods such as hovering, diving and sound-making with its wings to drive avian prey out of hiding (Cramp 1985). In addition, it will pick unfledged birds from nests (Schaefer 2004). The tawny owl hearing is important when hunting (Cramp 1985), and this might suggest that the tawny owl have been successful in localization and capturing of avian prey during the night by using bird vocalization.



### **4.3 Prey handling in the nest**

The probability of the adult female assisting in feeding was affected by both age of the nestling and prey body mass. As the nestlings grew older, they were capable of feeding unassisted more frequently. As the prey items were larger the probability of the female to assist feeding were larger. A similar pattern was found by Stave (2015) and by Sand (2016). A previous study of nine raptor species found that type and size of prey influenced the probability of when the female assisted feeding (Sonerud et al. 2014b). When the prey items were larger the female were more likely to assist feeding when the prey item were delivered at the nest (Sonerud et al. 2014b).

The result in this study is in line with the feeding constraint hypothesis, which states that an inability of young nestlings to ingest prey included in the diet of older nestlings, predicts that the extent of preparation would increase with prey size and decrease with age of the nestlings (Slagsvold & Wiebe 2007; Steen et al. 2010). As tawny owl nestlings hatch asynchronously (Hardey et al. 2006), the parents have to provide more feeding assistance to the smaller siblings when the parents deliver larger prey as that is more efficient (Slagsvold & Wiebe 2007). In altricial birds the type of prey selected by the parents might affect the time and energy spent on hunting, preparing prey and assist feeding for the nestlings, which in turn might affect their provisioning rate (Steen et al. 2011). As raptors take relatively large prey items, they optimize the number of prey items and the amount of prey mass delivered to the nestlings (Steen et al. 2011). To ensure that smaller siblings will not have a decreased survival chance compared to the larger siblings, parents should allocate prey items and assist feeding for the smallest siblings. As nestlings grow older and larger their demand for food increases (Barba et al. 2009). Therefore, it might be more profitable for foraging parents to deliver larger prey items when the nestlings are older (Slagsvold & Wiebe 2007). In broods with nestlings of different age the prey delivered were larger than broods with nestlings of the same age, which will reduce the survival chance of the smallest nestlings (Slagsvold & Wiebe 2007). In the nest box at Norderås, where there were five nestlings, it might have been an age difference of more than a week between the youngest and oldest nestlings.

The results in my study shows that the female stopped assisting the nestling to ingest mammals before birds. This is consistence with findings of Sonerud et al. (2014b). The efficiency with which a raptor nestling can ingest a prey item unassisted varies greatly among different types and sizes of prey (Steen 2010). The nestlings would be more likely to ingest prey items unassisted if the prey item is cylindrical with small appendages or limbs, like shrews and voles, than with prey items with large appendages or limbs that also will need to be plucked, like birds (Sonerud et al. 2013). The nestlings had an higher probability of feeding unassisted if the prey items were smaller within the same type (Sonerud et al. 2013). Therefore, the need for assistance would vary with prey type and size of prey (Steen 2010).

In the northern goshawk (*Accipiter gentilis*), the female decreased the amount of assisted feeding effort as the nestling aged (Byholm et al. 2011). If there was a higher availability than demand of food, the female assisted feeding more often (Byholm et al. 2011). This suggests that the higher provisioning rate of prey items from the male, the longer could the female delay her participation in hunting or even abstain from hunting (Eldegard & Sonerud 2009). This may explain why the tawny owl female seemed to assist feeding for a longer period in the nest at Jeksrud, compared to the other nests. At Jeksrud there was only one nestling, and therefore a lower demand for prey items, which gave the female the opportunity to assist feeding as she did not have to hunt for prey items for several nestlings. This is called a biological error in the model.

The classification of feeder as “female” or “nestling” depended on if we observed the nestling to swallow the prey. By applying this method, it was impossible to classify if the female in the nest box at Hauger assisted feeding or if the nestling fed unassisted before the nestling were 19 days old. This is called a methodical error. Both the biological and the methodical errors might make the switch from assisted feeding to feeding unassisted being inaccurate.

#### 4.4 Consumed prey mass per nestling per day

The non-linear model with nestling age as explanatory variable showed a peak in prey mass delivered when the nestlings were estimated to be 24 days old. The linear model with season as explanatory variable, which was the best model, showed that the consumed prey mass per nestling per day (24 h) increased throughout the monitoring period started on 22 April. The non-linear model with season as an explanatory variable showed a slow exponential pattern as the season progressed, but this pattern was only a trend. Cramp (1985) found that the feeding rate of tawny owls was largest when the nestlings were 11-25 days old. According to Steen et al. (2012), some raptors adjust the prey mass delivered to the age and needs of the nestlings.

The average fledging age in my study was 31 days, but one nestling at Norderås and one nestling at Hauger was never monitored until fledging because of some technical difficulties. In England, Coles and Petty (1997), found the averaged fledging age to be 32 days in a year with a low vole population. Cramp (1985) stated that the average time of fledging by the tawny owl nestlings are when they are about 25-30 days old. The average fledging age of my study, is in-between what is found in other studies. The nestling age in my study was estimated from videos, which might cause some inaccuracy. This study also determined age from the youngest nestling, which may differ from the oldest nestling by up to a week (Hardey et al. 2006).

I found a trend for prey mass delivered per nestling per day as a function of nestling age. In the great tit (*Parus major*), Barba et al. (2009) found that feeding rates usually increased with nestling age for some time, before it decreased as the nestlings approached their maximum body mass. This has been shown for some non-raptorial birds (Grundel 1987; Blondel et al. 1991; Barba et al. 2009). For the Eurasian kestrel, Steen et al. (2012) found a non-linear trend between prey mass delivered per nestling per day and nestling age, was shaped like an inverted U. Southern (1954) showed that the parents of the tawny owl continued to provide food for their nestlings a long time after fledging. The trend found, might be a consequence of the female trying force the nestlings to leave the nest box by starving them. Even though this test only considered data before any nestlings fledged, it still contained a few days from the nest box at Norderås where the female possibly starved her nestlings. This would potentially make some noise in this test, and might give some inaccurate results.

## 5. Conclusion

My study shows the diet of tawny owls to consists of mammals, birds, amphibians, reptiles, earthworms and insects (both larvae and fully grown), and thus confirms the tawny owl to be a food generalist. The probability of the female to assist feeding increased with prey body mass and decreased with nestling age, and the probability of the female to assist feeding was lower for mammals than for birds as the nestling grew. For future studies, it would be interesting to find out how early the nestlings could ingest certain prey items unassisted and if certain prey items were ingested unassisted before other types. The method of classification for feeding assistance or ingesting prey unassisted could potentially give a biased result, because it depended on if I saw the nestling to swallow the prey. By applying a second additional camera that points down into the nest box, a less biased estimate than obtained in my study may be possible. This would be interesting to do for tawny owls as well as other raptors.

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## Appendix



**Appendix 1:** Delivery of a wood mouse by the tawny owl at the nest box at the locality Jeksrud

**Appendix 2:** Parameter estimates from the model showing the probability of at least one prey delivery per hour block (n = 1978, random effect = 3 nests,  $\Delta AIC = 0.00$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-5.5889	0.7240	-7.720	<0.0001
I(cos(2 * $\pi$ * Hour/24))	4.3500	0.7477	5.818	<0.0001
I(sin(2 * $\pi$ * Hour/24))	4.4007	1.0049	4.379	0.0002
I(cos(2 * 2 * $\pi$ * Hour/24))	2.0987	0.4085	5.137	<0.0001
I(sin(2 * 2 * $\pi$ * Hour/24))	-2.9693	0.8172	-3.633	0.0003
I(cos(3 * 2 * $\pi$ * Hour/24))	-2.1765	0.3657	-5.951	<0.0001
I(sin(3 * 2 * $\pi$ * Hour/24))	0.2098	0.2750	0.763	0.45

**Appendix 3:** Parameter estimates from the model showing the probability of at least one avian prey delivery per hour block (n = 1978, random effect = 3 nests,  $\Delta AIC = 0.00$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-14.5896	3.8808	-3.759	0.0002
I(cos(2 * $\pi$ * Hour/24))	11.8237	4.2578	2.777	0.0055
I(sin(2 * $\pi$ * Hour/24))	14.4327	5.0230	2.873	0.0041
I(cos(2 * 2 * $\pi$ * Hour/24))	3.6981	1.3980	2.645	0.0082
I(sin(2 * 2 * $\pi$ * Hour/24))	-10.4717	3.8964	-2.688	0.0072
I(cos(3 * 2 * $\pi$ * Hour/24))	-4.6775	1.2569	-3.721	0.0002

**Appendix 4:** Parameter estimates from the model showing the probability of at least one mammalian prey delivery per hour block (n = 1978, random effect = 3 nests,  $\Delta AIC = 0.00$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-5.5106	0.8126	-6.782	<0.0001
I(cos(2 * $\pi$ * Hour/24))	4.1041	0.8928	4.597	<0.0001
I(sin(2 * $\pi$ * Hour/24))	3.5447	1.1023	3.216	0.0013
I(cos(2 * 2 * $\pi$ * Hour/24))	1.6237	0.4393	3.696	0.0002
I(sin(2 * 2 * $\pi$ * Hour/24))	-2.5136	0.9465	-2.656	0.0079
I(cos(3 * 2 * $\pi$ * Hour/24))	-1.7177	0.3880	-4.427	<0.0001
I(sin(3 * 2 * $\pi$ * Hour/24))	0.2673	0.3379	0.791	0.43

**Appendix 5:** Parameter estimates from the model showing the probability of at least one prey delivery of wood mouse per hour block (n = 1978, random effect = 3 nests,  $\Delta\text{AIC} = 0.00$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-7.1896	1.3860	-5.187	<0.0001
I(cos(2 * $\pi$ * Hour/24))	4.6308	1.4131	3.277	0.0011
I(sin(2 * $\pi$ * Hour/24))	4.5734	1.8293	2.500	0.012
I(cos(2 * 2 * $\pi$ * Hour/24))	2.3986	0.7351	3.263	0.0011
I(sin(2 * 2 * $\pi$ * Hour/24))	-3.4745	1.4814	-2.345	0.019
I(cos(3 * 2 * $\pi$ * Hour/24))	-1.9774	0.6435	-3.073	0.0021
I(sin(3 * 2 * $\pi$ * Hour/24))	0.4366	0.4911	0.889	0.37

**Appendix 6:** Parameter estimates from the model showing the probability of at least one prey delivery of field vole per hour block (n = 1978, random effect = 3 nests,  $\Delta\text{AIC} = 0.00$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-5.2407	0.4596	-11.403	<0.0001
I(cos(2 * $\pi$ * Hour/24))	2.1346	0.4752	4.492	<0.0001
I(sin(2 * $\pi$ * Hour/24))	1.1090	0.3646	3.042	0.0024

**Appendix 7:** Parameter estimates from the model showing the probability of at least one prey delivery of common shrew per hour block (n = 1978, random effect = 3 nests,  $\Delta\text{AIC} = 0.54$ ).

	<b>Estimates</b>	<b>SE</b>	<b>z</b>	<b>p</b>
Intercept	-5.9005	0.6188	-9.535	<0.0001
I(cos(2 * $\pi$ * Hour/24))	3.1955	0.7145	4.472	<0.0001
I(sin(2 * $\pi$ * Hour/24))	0.2881	0.3646	0.790	0.43



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