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Diet, diel activity and prey handling in the tawny owl (*Strix aluco*)

Diett, døgnaktivitet og byttedyrhåndtering hos kattugle (*Strix aluco*)

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Abstract

I recorded prey deliveries and prey handling using video monitoring at three tawny owl (*Strix aluco*) nests from late april to late may in 2017, in Akershus county in southeast Norway. I registered a total of 455 prey items, where vertebrates accounted for 85.5 % of all prey items by number, and 99.8 % by prey body mass, and invertebrates accounted for 12.3 % by number and 0.2 % by prey body mass. Unidentified prey made up 2.2 % of all prey items by number. Mammals were the largest group of delivered prey, accounting for 68.4 % of all deliveries by number, and 76.2 % by prey body mass, and birds were the second largest group, accounting for 12.3 % of all deliveries by number, and 17.9 % by prey body mass. The wood mouse (*Apodemus sylvaticus*) was the most common prey, accounting for 20.4 % of all prey items by number, and 25.6 % by prey body mass. Most of the prey deliveries occurred during nighttime, with a peak in the probability of a prey item delivered within the hour block 22.00-22.59. The probability that the nestlings needed maternal assistance in ingesting prey increased with prey body mass and decreased with nestling age for any kind of prey and for mammalian prey, and decreased with nestling age for avian prey. Prey body mass delivered per 24 hour increased with nestling age. However, body mass of each prey did not increase with nestling age. Therefore more prey items and not larger items were delivered with increasing nestling age.

Sammendrag

Jeg registrerte byttedyrleveringer og byttedyrhåndtering av kattugle (*Strix aluco*) ved å benytte meg av videoobservasjon ved tre kattuglereir fra slutten av april til slutten av mai 2017, i Akershus fylke i Norge. Jeg registrerte totalt 455 byttedyr, hvorav vertebrater utgjorde 85.5 % av alle byttedyr i antall, og 99.8 % av den totale vekten av byttedyrene. Invertebrater utgjorde 12.3 % i antall og 0.2 % av vekten. Uidentifiserte byttedyr utgjorde 2.2 % i antall av alle byttedyr. Pattedyr var den største gruppen av leverte byttedyr, og utgjorde 68.4 % i antall, og 76.2 % av vekten. Fugler var den nest største gruppen, og utgjorde 12.3 % i antall og 17.9 % av vekten. Skogmus (*Apodemus sylvaticus*) var det vanligste byttedyret, og utgjorde 20.4 % i antall, og 25.6 % av vekten. De fleste av leveringene ble gjort om natten, med høyest sannsynlighet for levering av byttedyr i timeblokken 22.00-22.59. Sannsynligheten for at ungene fikk foringshjelphjelp av hunnen økte med byttedyrvekt og sank med alder på ungene totalt sett, og for pattedyr, og sank med alder for fugler. Byttedyrvekt levert per døgn økte med alder på ungene, men vekten på hvert byttedyr økte ikke. Med andre ord var det flere, og ikke større, byttedyr som ble levert med ungenes økte alder.

1. Introduction

Many studies have been conducted on the ecology of raptors (i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes)), including their diet, diel activity and prey handling (Cramp & Simmons 1980; Cramp 1985). However, our knowledge of the diet of raptors has mainly come from analyses of pellets and remains of prey found at nest sites (Cramp 1985). This way of studying the diet of raptors might not give a complete picture of what kinds of prey items they ingest, because using only pellets and remains of prey, may give a biased estimate of the diet (Slagsvold et al. 2010). A potential error might be overestimating avian prey and large prey, while underestimating mammalian and smaller prey, including invertebrates (Simmons et al. 1991; Slagsvold et al. 2010).

One way to achieve a more complete picture of a raptor's diet, is using video monitoring of prey deliveries at the nests (Lewis et al. 2004). This would allow a visual recording of the actual deliveries, making it possible to see the prey items being delivered firsthand. This method also has the benefit of providing additional information about the raptor being studied. By continuously monitoring and recording events that take place at the nest, details about prey handling and diel activity can be revealed. Lately, it has therefore become more common to use video monitoring when studying prey deliveries in raptors (e.g. Slagsvold et al. 2010; Sonerud et al. 2014a).

The tawny owl is a medium-sized, resident, territorial, and nocturnal owl that is found throughout the Palearctic region (Cramp 1985; Jedrzejewski et al. 1996). It can be found in a diverse range of habitats, including forest areas, farmland, and urban areas (Cramp 1985; Hirons 1985; Obuch 2011). It is the most common owl in Europe (Zawadzka & Zawadzki 2007), and in Norway it is found in the lowlands in eastern Norway, and in the coastal areas as far north as Trøndelag county (Sonerud 1994). The tawny owl is a food generalist with a broad diet (e.g Galeotti 1990; Goszczynski et al. 1993; Sunde et al. 2001; Zawadzka & Zawadzki 2007), including mammals, birds, amphibians and invertebrates, depending on the availability of different prey types (Cramp 1985). The broad diet of the tawny owl probably makes it adaptable to fluctuations in the densities of different prey species, though it has been reported from Finland that its breeding success may vary according to the availability of small mammals (Karell et al. 2009). The tawny owl hunts mostly by using look-out posts and a sit-and-wait tactic (Southern 1954; Redpath 1995), although hunting in flight has also been reported (Nilsson 1978). Raptors have asymmetrical parental roles where in most species the female broods and feed the nestlings, and the male hunts, only assisted by the female towards the end of the nestling period, if at all (Sonerud et al. 2014b).

I studied the diet, diel activity, and prey handling of tawny owls in Akershus county, during the breeding season of 2017. I conducted my study by video monitoring three tawny owl nests from the beginning of the nestling period and until all the nestlings had fledged. My main

goals were to study i) what prey species are delivered to the tawny owl nests, ii) at what time of day are the prey items are delivered, iii) what factors influence whether or not the tawny owl nestlings feed with or without assistance from the female parent, and iv) the amount of prey mass delivered to the nestlings.

2. Methods

2.1 Study area

This study was conducted in Ås county in south-eastern Norway from late April to early June in 2017. Three nests of tawny owl were chosen at the locations Hauger, Kroer and Norderås (Figure 1), and all were nest boxes. The distances between the boxes ranged from 12.6 to 18.0 km. The nest box location at Hauger had deciduous forest to the north, agricultural land to the south, and mixed forests to the west and east (Vik 2017). The nest box at Kroer was located at the border between a field and an area of coniferous forest (Sand 2016). The nest box at Norderås was located in a small patch of deciduous forest that was surrounded by fields to the west and south, and forest to the east and north (Sand 2016).
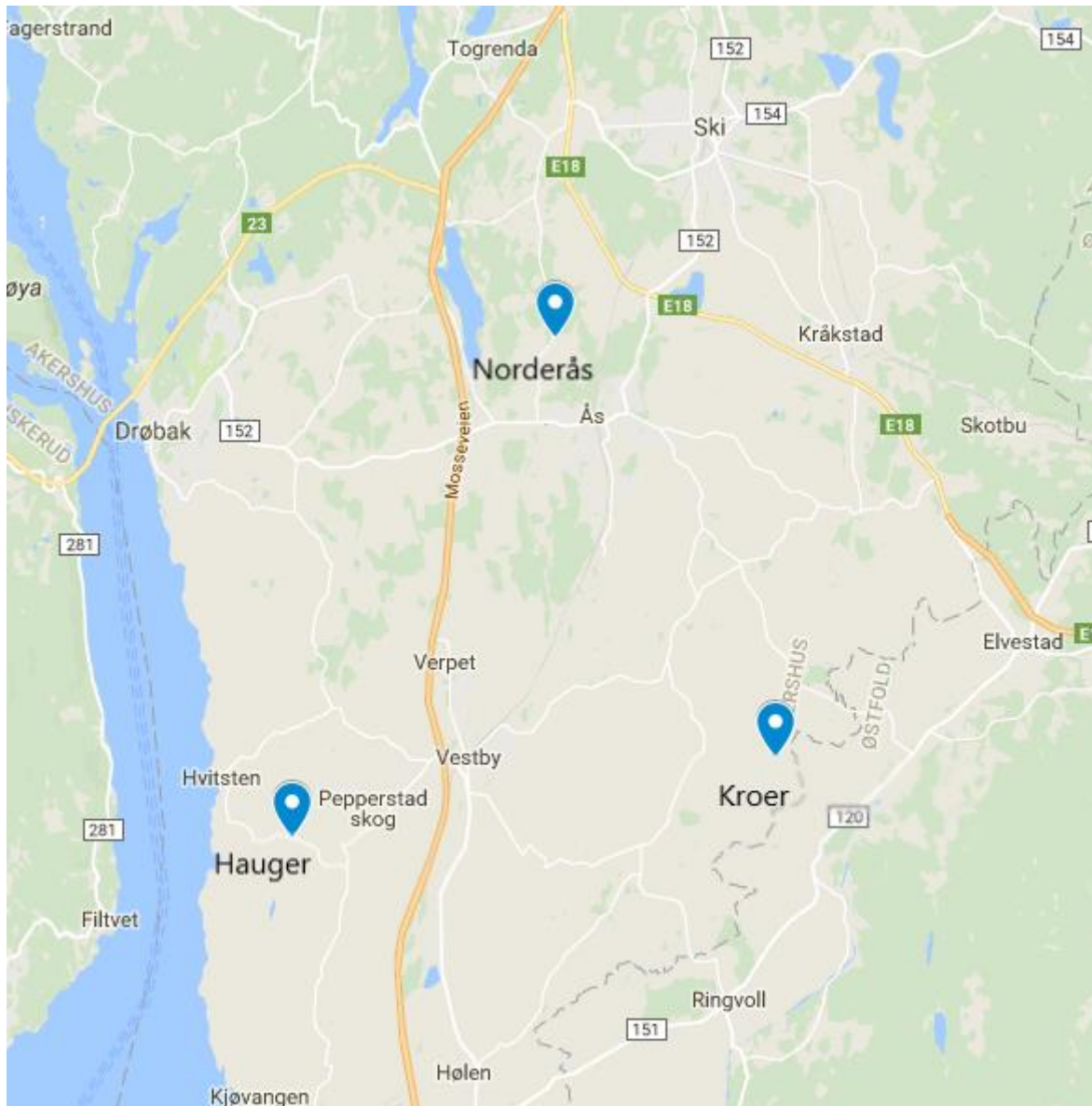
Figure 1: The location of the three nest boxes used in this study.

2.2 Video monitoring

The first day of field work (20 April) confirmed that all nest boxes had owl activity; the boxes at Hauger and Kroer contained eggs, whereas the box at Norderås already contained nestlings. To monitor the nests, I used a modification of the design described by Steen (2009). A camera was attached to the inside of each nest box, and had a wide angle lens in order to record the nest box entrance and part of the inside. The objective of the monitoring was to have recordings showing the parent with prey entering the box, and also to show the parent feeding the nestlings, in case it would be difficult to interpret what kind of prey was delivered, based only on the arrival of the parent owl. To be able to record in poor light conditions, expecting most deliveries to occur at nightime, a mini charged-coupled device (CCD) with infrared light

was used at all locations. A mini digital video recorder (DVR) connected to the camera was hidden on the ground, together with a 12 V 80AH or 12 V 60AH battery. The batteries and SD memory cards needed to be changed each week, and hiding this equipment on the ground made it possible to do this work without disturbing the tawny owls. The mini DVRs that were used was Secumate H.264 Mini Portable DVRs. The recordings were saved on 32 GB SD cards.

In order to capture on video only what was the most relevant information for my study, the cameras were set up to record 5 s before a parent entered the nest box, and then to continue to record another 10 s after the event that triggered the recording, using video motion detection (VMD). This was done so that I would be able to record the moment when the parent owl entered the box, and also some time after entering. This would give me enough images to reveal both what kind of prey were delivered, and the way the prey were handled in the nest. This was done successfully at Hauger and Kroer. However, regretfully, at Norderås it was discovered after some time that the camera had not been set ut to record the first 5 s mentioned above. The settings on the camera were then changed to fix this problem, but when reviewing the video clips for the analysis after the monitoring period was completed, I came to the conclusion that about half of the video material from this location was impossible to analyze. In short, the clips that could not be analysed lacked the important information I needed from the moment when the owl entered the nest box, making it impossibe to see what kind of prey was delivered.

2.3 Video analysis

The video clips lasted from a few seconds to several minutes, and made up a total of 100 hours, 40 minutes and 49 seconds that were recorded during the monitoring period. I went through all of these clips in order to separate the clips that showed prey deliveries from those that did not. Thereafter, I watched together with Geir A. Sonerud and Vidar Selås the clips that I had sorted out, to identify the prey items delivered, preferably to species level, or to the lowest possible taxa. This identification was based on the prey item's body size, colouration, fur structure, head shape, ear size, tail length, eye size, beak shape and size, plumage, tarsus and overall appearance. For this analysis, the video clips were prospected on a relatively large monitor, about 50 inches.

I have chosen not to specify shrews (Soricidae) or frogs (*Rana sp*.) to species level. One shrew was clearly a Eurasian water shrew (*Neomys fodiens*), and identified as such, but the rest, although believed to be common shrews (*Sorex araneus*), could potentially also be Eurasian water shrews, or Eurasian pygmy shrews (*Sorex minutus*). Most of the frogs were believed to be common frogs (*Rana temporaria*), but these could potentially also be moor frogs (*Rana arvalis*). The prey items identified as *Apodemus sp*. were registered as wood mice (*Apodemus sylvaticus*), because an annual snap trapping program that has been going on in Ås

from 1993 to present, has shown that this is the only *Apodemus* species caught at this location (Geir A. Sonerud, pers. comm.).

The date and hour of each delivery was registered by looking at the time stamp on the video clip. Other important parameters that were registered when going through the clips, in addition to identifying the prey items, were nest ID, whether or not the nestlings were assisted by the female parent when ingesting the prey, whether the prey had been decapitated or eaten at, and the age of the nestlings at the time of each delivery. The age of the nestlings was defined as the oldest nestling in each brood; a nestling at the age of 1 day from a certain brood, was the day the first nestling hatched. Which parent was defined as the deliverer of the prey was based on its behaviour; if the deliverer went inside the box, I always defined the deliverer to be the female.

2.4 Estimation of prey body mass

To estimate the prey body mass of mammalian prey, I used data from the annual snap trapping conducted at Ås from 1993 to present (Geir A. Sonerud, pers. comm.) For avian prey, the prey body mass was obtained from data most relevant to the breeding season in Fennoscandia (Cramp 1988, 1992; Cramp & Perrins 1993, 1994; Selås 2001). For reptiles and frogs, the same method was used as for mammals (Vidar Selås and Geir A. Sonerud, pers. comm.) In addition, the frogs were divided into two groups, small and large, based on their appearance on the video screen, and they were given estimated body masses accordingly. The body mass of earthworms was obtained from Stave (2015), and the body mass of insects from Itämies and Korpimäki (1987). The few prey items that could not be identified to any taxa were not assigned any body mass, and were ignored in the analyses involving prey mass.

During the observations of prey deliveries it was often difficult to tell wether or not the prey had been decapitated prior to delivery, and therefore also difficult to estimate the body mass of the prey. This could potentially become a problem making calculations and analyses involving prey body mass. However, because it was extremely rare that I saw prey items that had been decapitated, I decided to set net prey body mass to gross prey body mass, as if the prey had not been decapitated. In other words, when uncertain, I assumed that the prey item had not been decapitated prior to delivery, and assigned it the body mass it would have had, if it had not been decapitated, i.e. the actual mass of the prey before being captured. For the prey items where decapitation was evident, 12.9 % of the assigned body mass was subtracted for avian prey, and 16.5 % was subtracted for mammalian prey (Sonerud et al. 2014b).

2.5 Statistical analysis

For statistical analysis, the software program R version 3.3.3 (R Development Core Team 2017) was used. From 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. Both logistic and linear regression models were used. Figures were constructed using R.

The circadian activity rhythm of the tawny owls were analysed by the use of the cosinor method, where the periodic components of time series were set as sine and cosine functions (Pita et al. 2011). The day was divided into 24 hour blocks, from 0 to 23 for each 24-hour period, making the sample unit each hour of the day. This was termed x in the models. The probability of a prey delivery within a certain hour block was set to be the response variable, and if one or more deliveries occurred within an hourblock, it was scored as «yes», and if no deliveries occurred, it was scored as «no». This was therefore a conservative test. The random effect was a correction for nest ID, and was called ε in the models. The models were ranked by AIC values (Burnham & Anderson 2002). The models (M_1-M_4) were such:

M_0: $logit\big(f(x)\big) = a_0 + \varepsilon$

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

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

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

A test was done for the probability that the nestlings would feed unassisted rather than being assisted by the female parent. For this test, prey mass (g) and nestling age (d) were explanatory variables. Another test was done for the probability of unassisted feeding separately for mammalian and avian prey, with nestling age (d) as explanatory variable. Finally, a test was done for prey mass delivered per nestling per day (24 h), and for mass (g) of each prey delivered, with nestling age (d) as the explanatory variable. Average prey body mass was estimated by controlling for nest ID (with and without Norderås) and nestling age.

3. Results

3.1 Diet composition

In total, I recorded the delivery of 455 prey items at the three nests, and these consisted of a wide variety of species (Table 1). Vertebrates, represented by mammals, birds, amphibians and reptiles, accounted for 85.5 % of all prey, whereas invertebrates (earth worms and insects) accounted for 12.3 %. Unidentified prey items made up 2.2 % of the deliveries. Within vertebrates, mammals were the largest group by number, accounting for 68.4 % of all deliveries, and within mammals, wood mouse was the most common prey (20.4 %), followed

by shrews (16.7 %). Birds were the second largest group of prey, with 12.3 % of all deliveries, followed by amphibians (4.6 %) and reptiles (0.2 %). In terms of prey mass of identified prey, vertebrates accounted for 99.8 %, and invertebrates 0.2 % (Table 2). Within vertebrates, mammals were the largest group, accounting for 76.2 %. Within mammals, wood mouse contributed the most in mass with 25.6 %, followed by bank vole (*Myodes glareous*) (15.3 %) and field vole (*Microtus agrestis*) (12.7 %). Shrews accounted for 8.5 % of total prey mass. Birds were the second largest group with 17.9 % of total prey mass delivered, followed by amphibians (5.6 %) and reptiles (0.06 %). The avarage prey body mass delivered per nestling per day (24 h), corrected for nest ID, was 19.9 g for all three nests, and 22.2 g counting only Hauger and Kroer.

Of the three tawny owl nests, Hauger had the highest percentage of wood mice by number, with 42.5 %, Kroer the highest percentage of shrews, with 28.4 %, and Norderås had the highest percentage of invertebrate prey with 35.7 %.

Table 1: Number of prey items delivered at three tawny owl nests (Hauger, Kroer and Norderås) during the breeding season of 2017, with percentages by number of prey items for each nest, as well as in total. See page 8.

Table 2: Estimated prey body mass (g) delivered at three tawny owl nests (Hauger, Kroer and Norderås) during the breeding season of 2017, with percentages by prey mass for each nest, as well as in total. See page 9.

Species	Hauger		Kroer		Norderås		Total	
	No.	%	No.	%	No.	%	No.	%
Water shrew (*Neomys fodiens*)	0	0.0	1	0.5	0	0.0	1	0.2
Shrew (Soricidae)	2	1.3	57	27.9	16	16.3	75	16.5
Bank vole (*Myodes glareous*)	21	13.7	38	18.6	4	4.1	63	13.8
Field vole (*Microtus agrestis*)	16	10.5	16	7.8	4	4.1	36	7.9
Bank vole or field vole	1	0.7	13	6.4	2	2.0	16	3.5
Bank vole or wood mouse	0	0.0	1	0.5	0	0.0	1	0.2
Wood mouse (*Apodemus sylvaticus*)	65	42.5	19	9.3	9	9.2	93	20.4
Norway rat (*Rattus norvegicus*)	1	0.7	2	1.0	0	0.0	3	0.7
Unidentified small rodent (Rodentia)	0	0.0	3	1.5	3	3.1	6	1.3
Unidentified small mammal (Mammalia)	0	0.0	7	3.4	10	10.2	17	3.7
Mammals total	**106**	**69.3**	**157**	**77.0**	**48**	**49.0**	**311**	**68.4**
White wagtail (*Motacilla alba*)	1	0.7	0	0.0	0	0.0	1	0.2
European robin (*Erithacus rubecula*)	1	0.7	0	0.0	0	0.0	1	0.2
Northern wheatear (*Oenanthe oenanthe*)	0	0.0	1	0.5	0	0.0	1	0.2
Common blackbird (*Turdus merula*)	0	0.0	1	0.5	0	0.0	1	0.2
Redwing (*Turdus iliacus*)	0	0.0	1	0.5	0	0.0	1	0.2
Song thrush (*Turdus philomelos*)	1	0.7	2	1.0	0	0.0	3	0.7
Unidentified thrush (*Turdus sp.*)	2	1.3	4	2.0	1	1.0	7	1.5
Blackcap (*Sylvia atricapilla*)	1	0.7	0	0.0	0	0.0	1	0.2
Willow warbler (*Phylloscopus trochilus*)	1	0.7	2	1.0	0	0.0	3	0.7
Unidentified warbler *(*Sylvidae*)*	2	1.3	1	0.5	0	0.0	3	0.7
Coal tit (*Periparus ater*)	0	0.0	1	0.5	0	0.0	1	0.2
European blue tit (*Cyanistes caeruleus*)	1	0.7	0	0.0	1	1.0	2	0.4
Great tit (*Parus major*)	0	0.0	0	0.0	2	2.0	2	0.4
Unidentified tit (Paridae)	3	2.0	1	0.5	0	0.0	4	0.9
Common chaffinch (*Fringilla coelebs*)	0	0.0	3	1.5	0	0.0	3	0.7
Unidentified crossbill (*Loxia sp.*)	0	0.0	1	0.5	0	0.0	1	0.2
Unidentified small bird (Aves)	12	7.8	4	2.0	3	3.1	19	4.2
Unidentified bird (Aves)	1	0.7	1	0.5	0	0.0	2	0.4
Birds total	**26**	**17.0**	**23**	**11.3**	**7**	**7.1**	**56**	**12.3**
Frog (*Rana sp.*)	2	1.3	16	7.8	2	2.0	20	4.4
Smooth newt (*Lissotriton vulgaris*)	0	0.0	0	0.0	1	1.0	1	0.2
Amphibians total	**2**	**1.3**	**16**	**7.8**	**3**	**3.1**	**21**	**4.6**
Common lizard (*Zootoca vivipara*)	0	0.0	1	0.5	0	0.0	1	0.2
Reptiles total	**0**	**0.0**	**1**	**0.5**	**0**	**0.0**	**1**	**0.2**
Earthworm (Lumbricidae)	6	3.9	2	1.0	11	11.2	19	4.2
Dor beetle (*Anoplotrupes stercorosus*)	1	0.7	0	0.0	0	0.0	1	0.2
Unidentified beetle (Coleoptera*)*	5	3.3	0	0.0	3	3.1	8	1.8
Unidentified Lepidoptera larvae	3	2.0	0	0.0	0	0.0	3	0.7
Unidentified insect (Insecta)	3	2.0	0	0.0	9	9.2	12	2.6
Unidentified insect larvae (Insecta)	1	0.7	0	0.0	12	12.2	13	2.9
Invertebrates total	**19**	**12.4**	**2**	**1.0**	**35**	**35.7**	**56**	**12.3**
Unidentified prey	0	0.0	5	2.5	5	5.1	10	2.2
Prey total	**153**	**100.0**	**204**	**100.0**	**98**	**100.0**	**455**	**100.0**

Species	Hauger		Kroer		Norderås		Total	
	g	%	g	%	g	%	g	%
Water shrew (*Neomys fodiens*)	0.0	0.0	15.0	0.3	0.0	0.0	15.0	0.2
Shrew (Soricidae)	20.0	0.6	570.0	12.7	160.0	13.4	750.0	8.3
Bank vole (*Myodes glareous*)	462.0	13.6	836.0	18.6	88.0	7.4	1386.0	15.3
Field vole (*Microtus agrestis*)	512.0	15.1	512.0	11.4	128.0	10.7	1152.0	12.7
Bank vole or field vole	27.0	0.8	351.0	7.8	54.0	4.5	432.0	4.8
Bank vole or wood mouse	0.0	0.0	23.5	0.5	0.0	0.0	23.5	0.3
Wood mouse (*Apodemus sylvaticus*)	1625.0	48.0	475.0	10.6	225.0	18.9	2325.0	25.6
Norway rat (*Rattus norvegicus*)	100.0	3.0	200.0	4.4	0.0	0.0	300.0	3.3
Unidentified small rodent (Rodentia)	0.0	0.0	78.9	1.8	78.9	6.6	157.8	1.7
Unidentified small mammal (Mammalia)	0.0	0.0	156.1	3.5	220.0	18.5	376.1	4.1
Mammals total	**2746.0**	**81.0**	**3217.5**	**71.5**	**953.9**	**80.1**	**6917.4**	**76.2**
White wagtail (*Motacilla alba*)	21.0	0.6	0.0	0.0	0.0	0.0	21.0	0.2
European robin (*Erithacus rubecula*)	18.0	0.5	0.0	0.0	0.0	0.0	18.0	0.2
Northern wheatear (*Oenanthe oenanthe*)	0.0	0.0	22.0	0.5	0.0	0.0	22.0	0.2
Common blackbird (*Turdus merula*)	0.0	0.0	95.0	2.1	0.0	0.0	95.0	1.0
Redwing (*Turdus iliacus*)	0.0	0.0	70.0	1.6	0.0	0.0	70.0	0.8
Song thrush (*Turdus philomelos*)	74.0	2.2	148.0	3.3	0.0	0.0	222.0	2.4
Unidentified thrush (*Turdus sp.*)	160.0	4.7	320.0	7.1	80.0	6.7	560.0	6.2
Blackcap (*Sylvia atricpilla*)	17.0	0.5	0.0	0.0	0.0	0.0	17.0	0.2
Willow warbler (*Phylloscopus trochilus*)	9.0	0.3	18.0	0.4	0.0	0.0	27.0	0.3
Unidentified warbler (Sylvidae)	20.0	0.6	10.0	0.2	0.0	0.0	30.0	0.3
Coal tit (*Periparus ate*r)	0.0	0.0	12.0	0.3	0.0	0.0	12.0	0.1
European blue tit (*Cyanistes caeruleus*)	11.0	0.3	0.0	0.0	11.0	0.9	22.0	0.2
Great tit (*Parus major*)	0.0	0.0	0.0	0.0	36.0	3.0	36.0	0.4
Unidentified tit (Paridae)	45.0	1.3	15.0	0.3	0.0	0.0	60.0	0.7
Common chaffinch (*Fringilla coelebs*)	0.0	0.0	69.0	1.5	0.0	0.0	69.0	0.8
Unidentified crossbill (*Loxia sp.*)	0.0	0.0	38.0	0.8	0.0	0.0	38.0	0.4
Unidentified small bird (Aves)	180.0	5.3	60.0	1.3	45.0	3.8	285.0	3.1
Unidentified bird (Aves)	25.0	0.7	0.0	0.0	0.0	0.0	25.0	0.3
Birds total	**580.0**	**17.1**	**877.0**	**19.5**	**172.0**	**14.4**	**1629.0**	**17.9**
Frog (*Rana sp.*)	55.0	1.6	400.0	8.9	50.0	4.2	505.0	5.6
Smooth newt (*Lissotriton vulgaris*)	0.0	0.0	0.0	0.0	2.0	0.2	2.0	0.02
Amphibians total	**55.0**	**1.6**	**400.0**	**8.9**	**52.0**	**4.4**	**507.0**	**5.6**
Common lizard (*Zootoca vivipara*)	0.0	0.0	5.0	0.1	0.0	0.0	5.0	0.06
Reptiles total	**0.0**	**0.0**	**5.0**	**0.1**	**0.0**	**0.0**	**5.0**	**0.06**
Earthworm (Lumbricidae)	4.8	0.1	1.6	0.04	8.8	0.7	15.2	0.2
Dor beetle (*Anoplotrupes stercorosus*)	0.2	0.006	0.0	0.0	0.0	0.0	0.2	0.002
Unidentified beetle (Coleoptera*)*	1.0	0.03	0.0	0.0	0.6	0.05	1.6	0.02
Unidentified Lepidoptera larvae	0.6	0.02	0.0	0.0	0.0	0.0	0.6	0.007
Unidentified insect (Insecta)	0.6	0.02	0.0	0.0	1.8	0.2	2.4	0.03
Unidentified insect larvae (Insecta)	0.2	0.006	0.0	0.0	2.4	0.2	2.6	0.03
Invertebrates total	**7.4**	**0.2**	**1.6**	**0.04**	**13.6**	**1.1**	**22.6**	**0.2**
Unidentified prey	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prey total	**3388.4**	**100.0**	**4501.1**	**100.0**	**1191.5**	**100.0**	**9081.0**	**100.0**

3.2 Time of day of prey deliveries

The average probability of any kind of prey delivery per hour, i.e. the average activity of the tawny owls, was 0.17, meaning that any activity above this level represents the owls main active period. The main activity period occurred in the hour blocks from 20.00-03.59, and hunting activity peaked in the hour block 22.00-22.59, with a value of 0.47 (Figure 2, Appendix 2). Although a considerably higher activity was displayed during nightime than during daytime, the activity level was not zero during the day; a few deliveries occured even then (Figure 2).
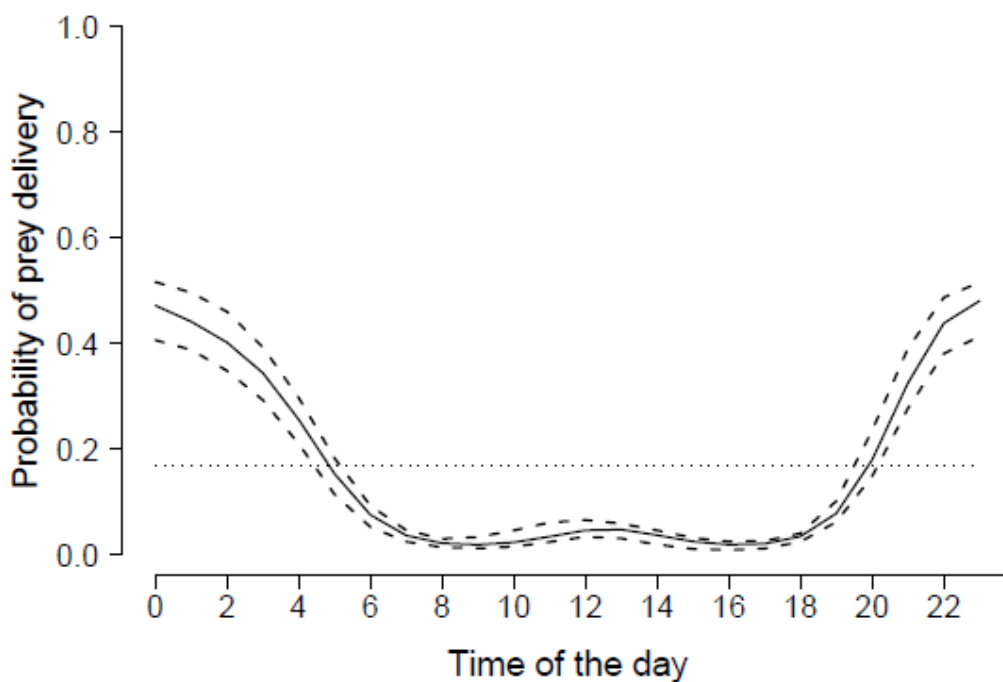
Figure 2: Probability of at least one prey delivery per hour block as a function of time of day (h) at three tawny owl nests, predicted from models of circadian activity rhythms. The two dashed lines represent the confidence interval, the dotted line is the midline estimating statistic of rhythm (MESOR).

The probability of a prey delivery per hour was in general higher for mammalian prey than for avian prey, with much higher values in the hour block it peaked (Figure 3, Appendix 3). The average activity level for mammalian prey was 0.12, and it peaked in the hour block 23.00-23.59, and then had a value of 0.37 (Figure 3).
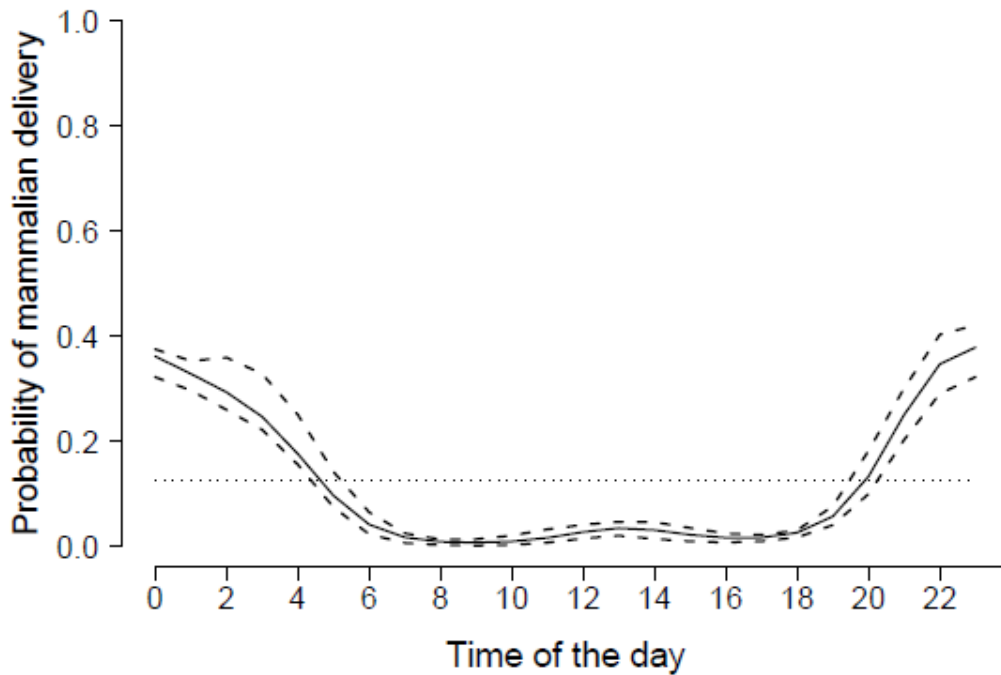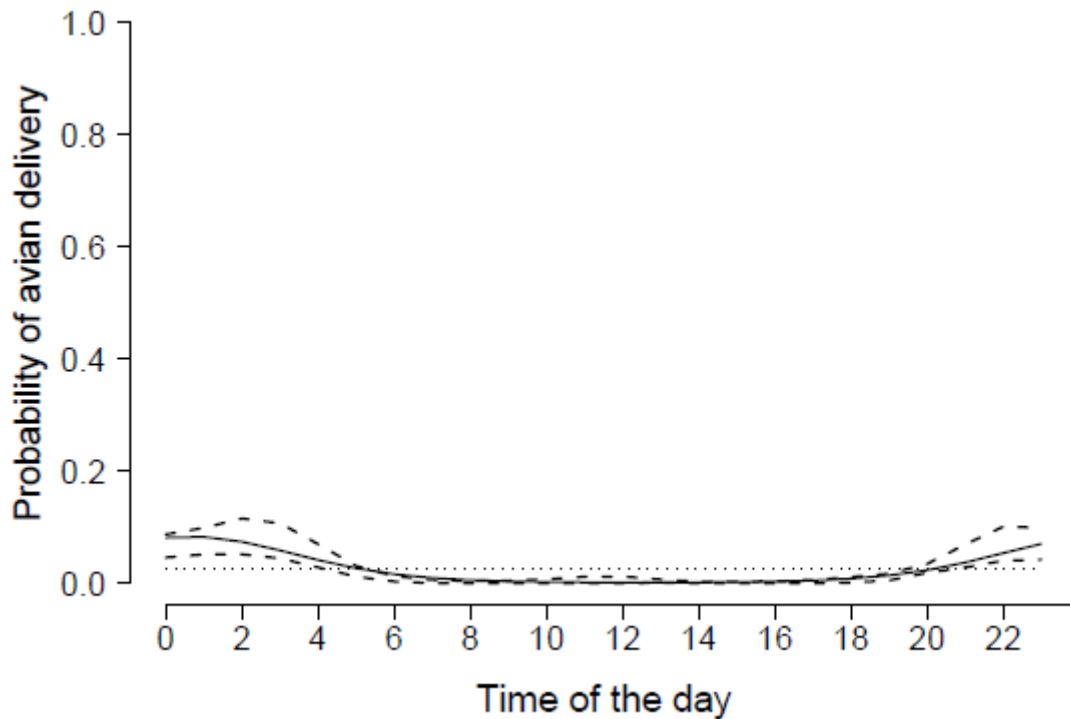
Figure 3: Probability of at least one mammalian prey delivery per hour block as a function of time of day (h) at three tawny owl nests, predicted from models of circadian activity rhythms. The two dashed lines represent the confidence interval, the dotted line is the midline estimating statistic of rhythm (MESOR).

For avian prey, the average activity level was 0.03. The highest values were still during the night, but with the highest probability reaching only 0.08 (Figure 4, Appendix 4). In addition, the peak occurred later than for mammals, in the hour block from 00.00-00.59. There was a very low probability that a bird was delivered during daytime (Figure 4).

Figure 4: Probability of at least one avian prey delivery per hour block as a function of time of day (h) at three tawny owl nests, predicted from models of circadian activity rhythms. The two dashed lines represent the confidence interval, the dotted line is the midline estimating statistic of rhythm (MESOR).

3.3 Prey handling in the nest

The model that best explained the probability of nestlings feeding on any kind of prey unassisted (AIC = 282.8), included both nestling age and prey body mass as explanatory variables (Table 3). The probability of unassisted feeding on any kind of prey decreased significantly with prey mass and increased significantly with nestling age (Table 3). Therefore, high nestling age and low prey mass predicted the highest probability that the nestlings would feed unassisted (Figure 5).
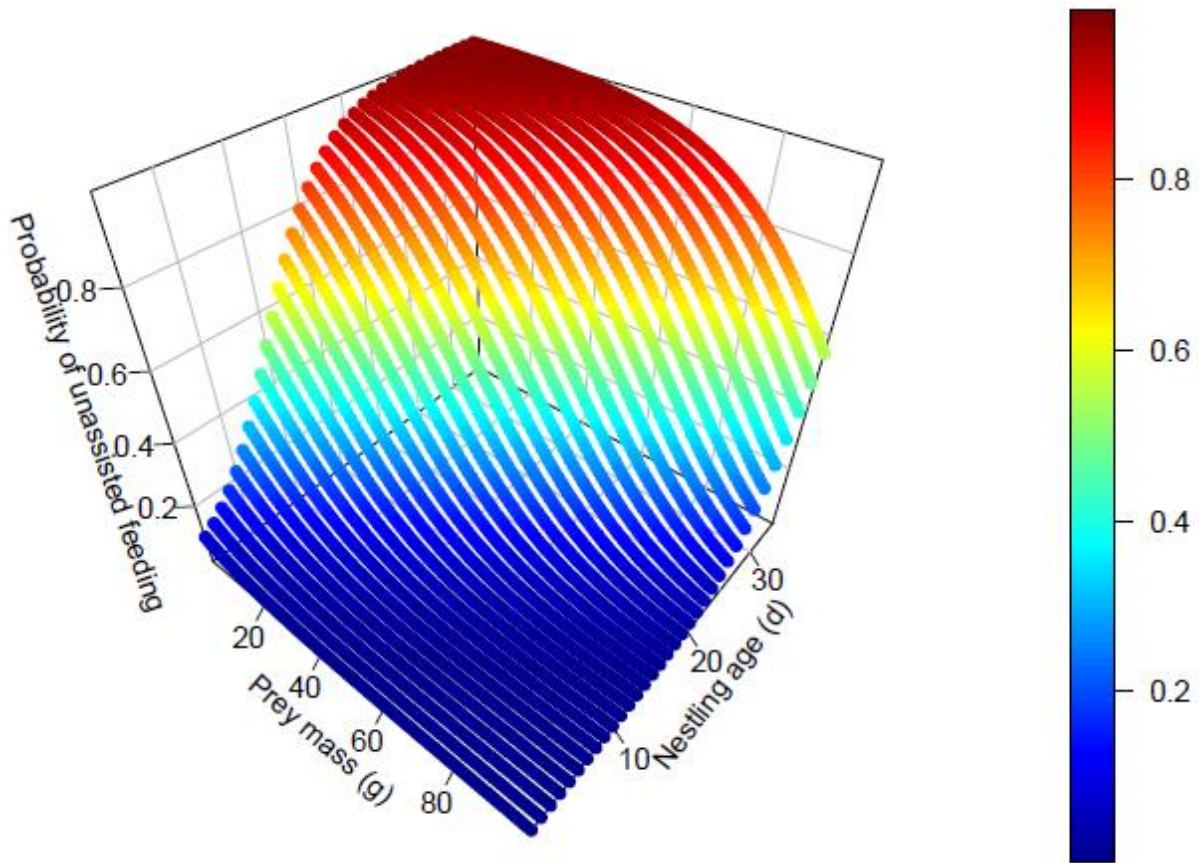
Figure 5: The probability that the tawny owl nestlings ingested any kind of prey unassisted as a function of prey mass and nestling age. Nestling age is defined as the age of the the first hatched nestling in a brood.

Table 3: Parameter estimates from the model of the probability that the tawny owl nestlings ingested a prey item unassisted as a function of nestling age (d) and prey body mass (g). The model is corrected for nest ID (n = 367, random effect = 3 nests).

	Estimate	**SE**	**z**	**p**
Intercept	-2.544	0.641	-3.971	<0.001
Nestling age	0.259	0.029	8.954	<0.001
Prey body mass	-0.061	0.011	-5.519	<0.001

The model that best explained the probability of nestlings feeding on mammals unassisted (AIC = 141.1) also included both nestling age and prey body mass as explanatory variables (Table 4). The probability of unassisted feeding on mammals decreased significantly with prey mass and increased significantly with nestling age (Table 4). Therefore, high nestling age

and low prey mass predicted the highest probability that the nestlings would feed unassisted (Figure 6).
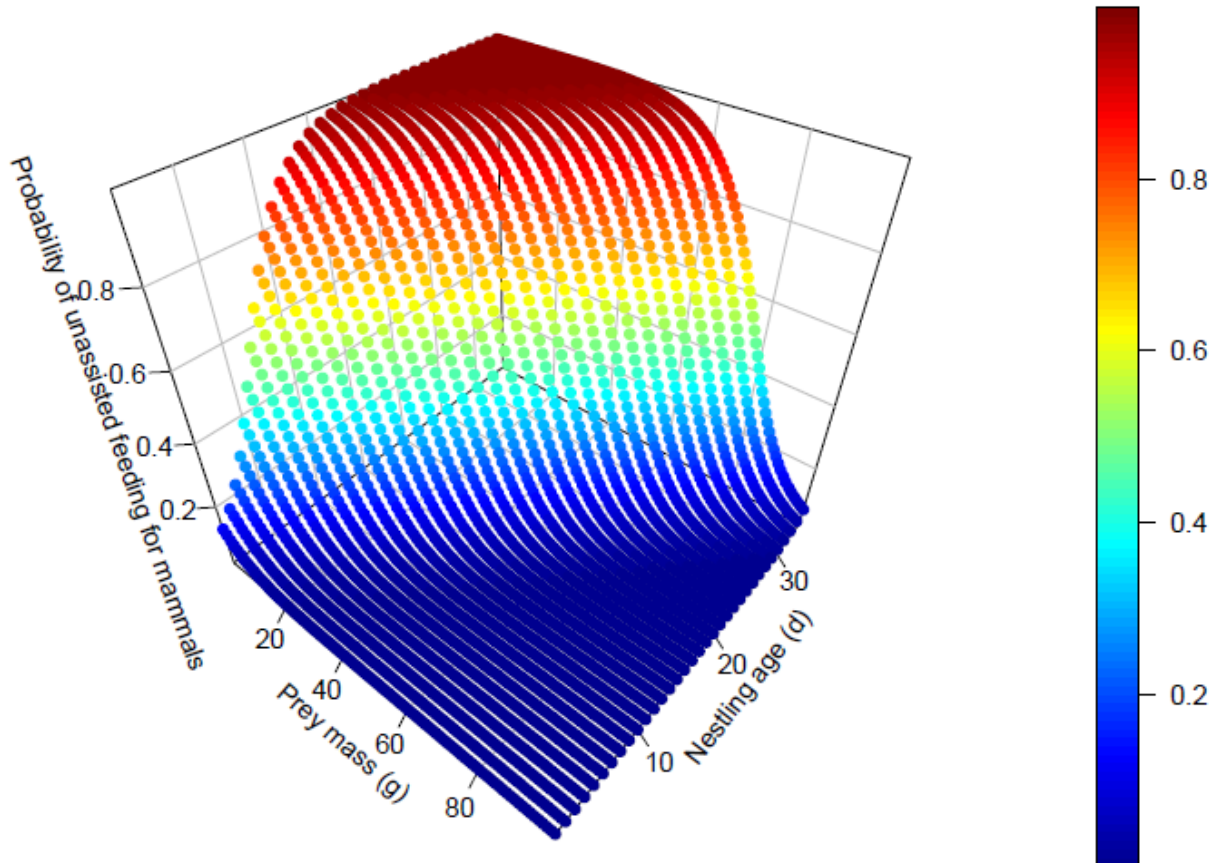

Figure 6: The probability that the tawny owl nestlings ingested mammalian prey unassisted as a function of prey mass and nestling age. Nestling age is defined as the age of the the first hatched nestling in a brood.

Table 4: Parameter estimates from the model of the probability that the tawny owl nestlings ingested a mammalian prey item unassisted as a function of nestling age (d) and prey body mass (g). The model is corrected for nest ID (n = 256, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.299	1.265	-1.817	0.069
Nestling age	0.363	0.051	7.067	<0.001
Prey body mass	-0.130	0.036	-3.560	<0.001

The model that best explained the probability of nestlings feeding on birds unassisted (AIC = 56.1) included only nestling age as the explanatory variable. The probability of unassisted feeding on birds was thus not affected by prey body mass, but did increase marginally non-significant with nestling age (Table 5). Therefore, high nestling age alone predicted a higher probability that the nestlings would feed unassisted (Figure 7).
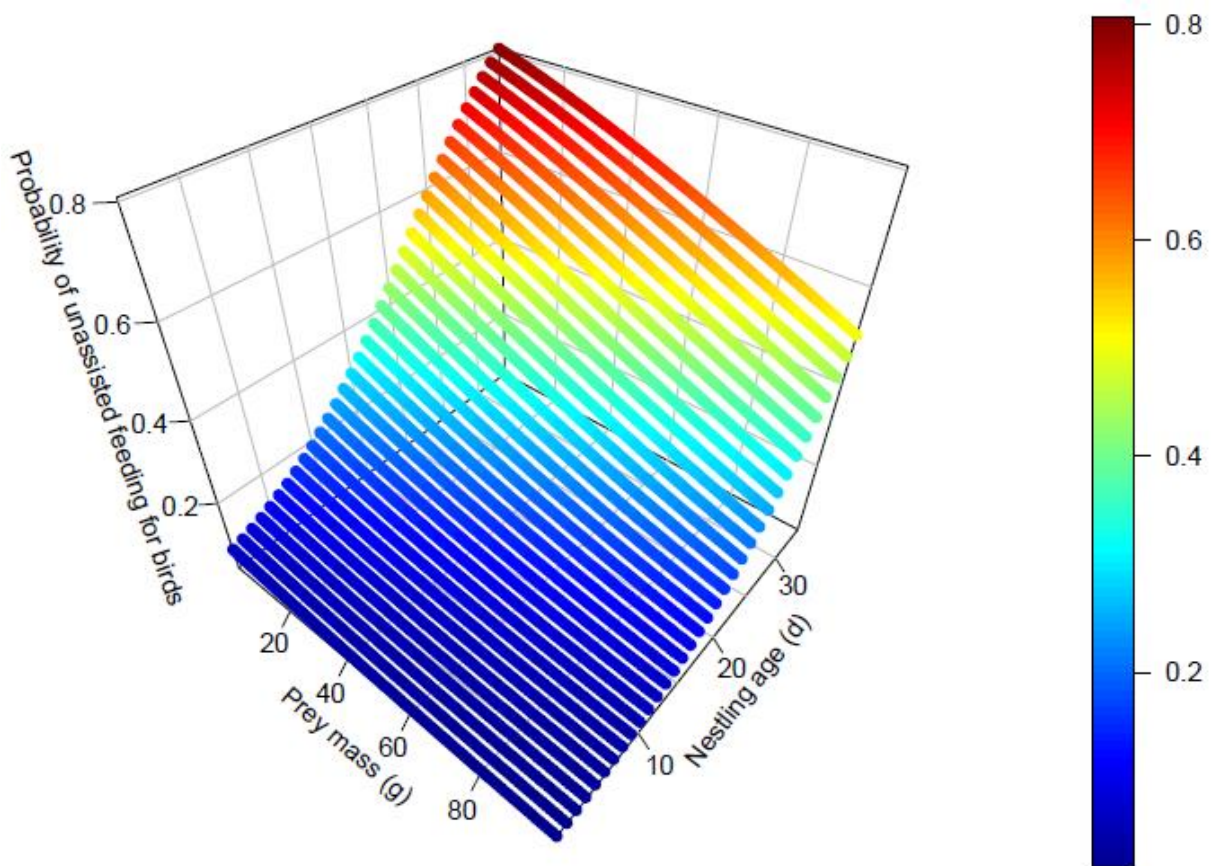

Figure 7: The probability that the tawny owl nestlings ingested avian prey unassisted as a function of prey mass and nestling age. Nestling age is defined as the age of the the first hatched nestling in a brood.

Table 5: Parameter estimates from the model of the probability that the tawny owl nestlings ingested an avian prey item unassisted as a function of nestling age (d). The model is corrected for nest ID (n = 41, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.684	1.440	-1.864	0.0623
Nestling age	0.102	0.061	1.670	0.0949

For any kind of prey, with nestling age as the only explanatory variable, the probability of feeding unassisted increased with nestling age (Figure 8). The switch, which is when the probability of feeding unassisted equals the probability of assisted feeding, occurred at about the age of 14 days. At the age of about 23 days, the probability of feeding unassisted had reached a value of 0.9, and it continued to increase even after this (Figure 8).
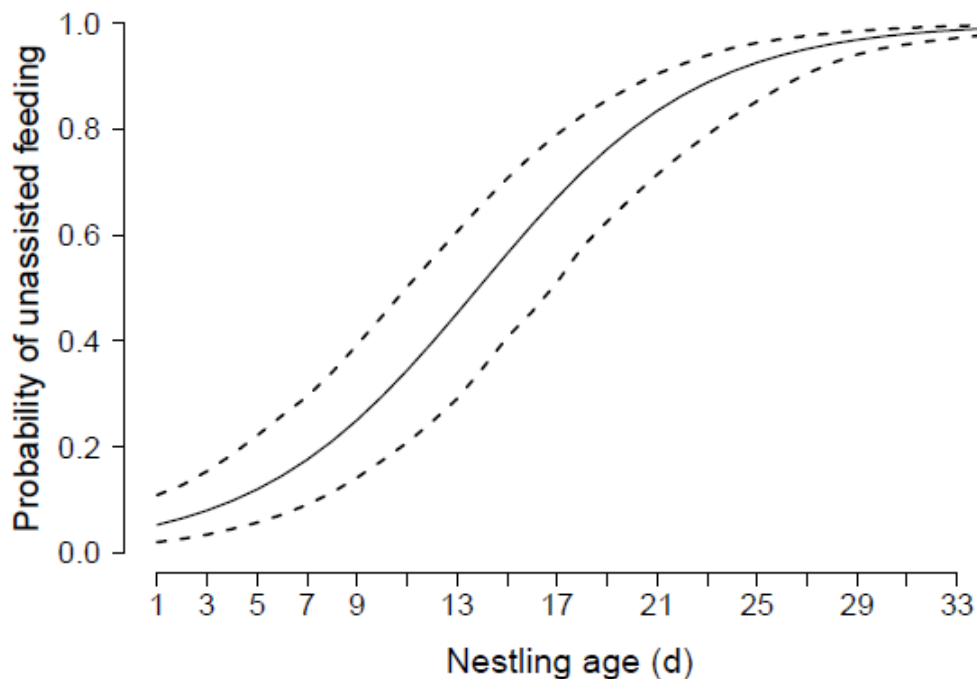

Figure 8: The probability that the tawny owl nestlings ingested any kind of prey unassisted as a function of nestling age. Nestling age is defined as the age of the first hatched nestling in a brood

For mammalian prey only, and with nestling age as the explanatory variabel, the increase in the probability of feeding unassisted was rapid from around a week of age, and this trend continued to around the age of 14 days, when the switch occurred (Figure 9). When the nestlings had reached the age of 20 days, more or less all mammalian prey were consumed without the aid of the female parent from here on.
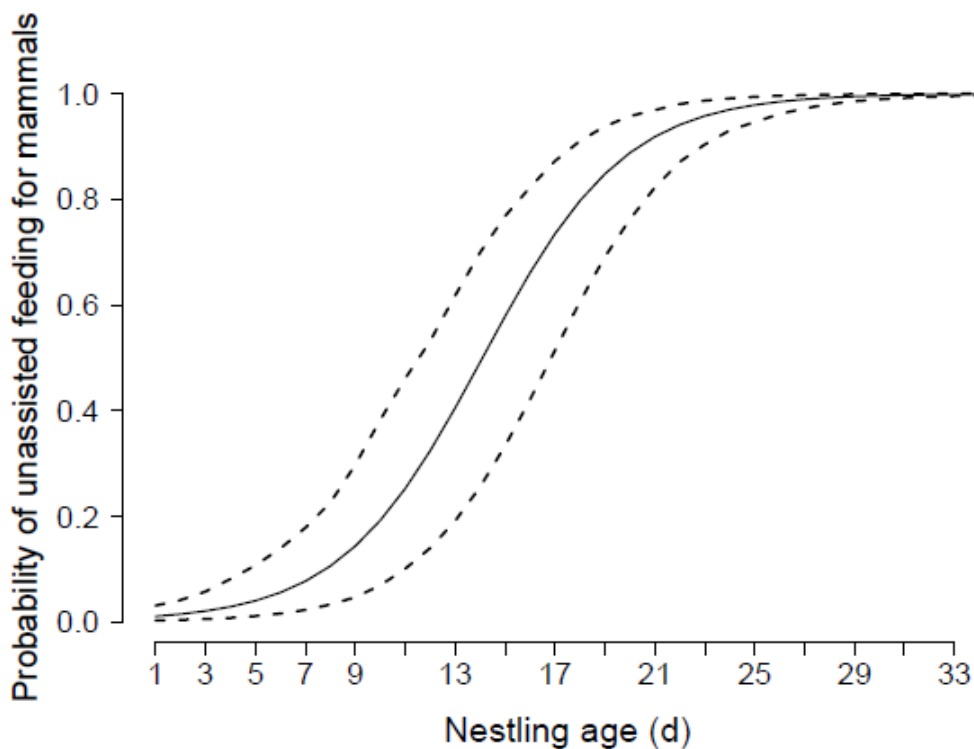

Figure 9: The probability that the tawny owl nestlings ingested mammalian prey unassisted as a function of nestling age. Nestling age is defined as the age of the first hatched nestling in a brood.

For avian prey only, the nestlings never reached as high a probability of feeding unassisted as for mammalian prey, and the prediction line looked different. For birds, there was instead a slow increase during the entire period, and the probability never exceeded 0.7 (Figure 9). This means that even when the nestlings had reached fledging age, they were still being assisted by the female parent when feeding on avian prey in about a third of the cases. The switch occurred considerably later than for mammalian prey, at around the age of 26 days (Figure 9).
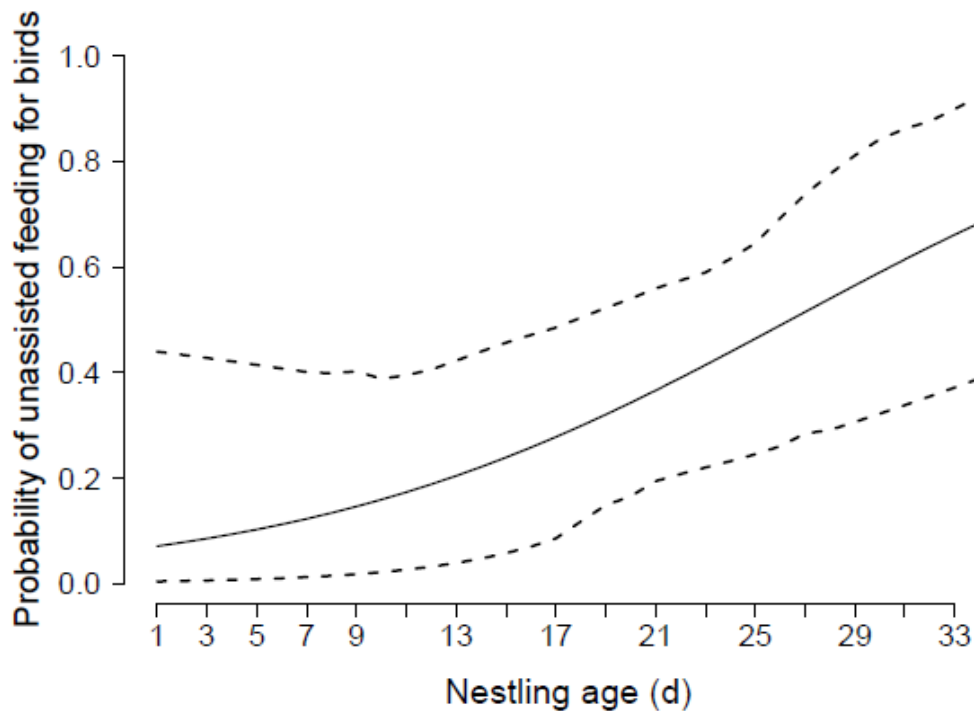
Figure 10: The probability that the tawny owl nestlings ingested avian prey unassisted as a function of nestling age. Nestling age is defined as the age of the first hatched nestling in a brood.

3.4 Prey mass delivered

To describe prey mass delivered per nestling per day (24 h), a linear and a a non-linear model were made, with prey mass (g) delivered per nestling per day (24 h) as the response variable, and with nestling age as the explanatory variable (Figure 11). These models only included the two nests for which there were complete data sets, thus Nordereås was not included (see methods). The best model to explain the results was the linear model (AIC = 539.1).

The prey mass delivered per nestling per day (24 h) increased as the nestlings grew older, from an estimated 30 g at the age of 4 days, to c 40 g at the age of 10 days, and c 60 g at the age of 25 days (Figure 11). These results show that the increase in delivered prey mass continued throughout the entire period, i.e until the nestlings fledged.
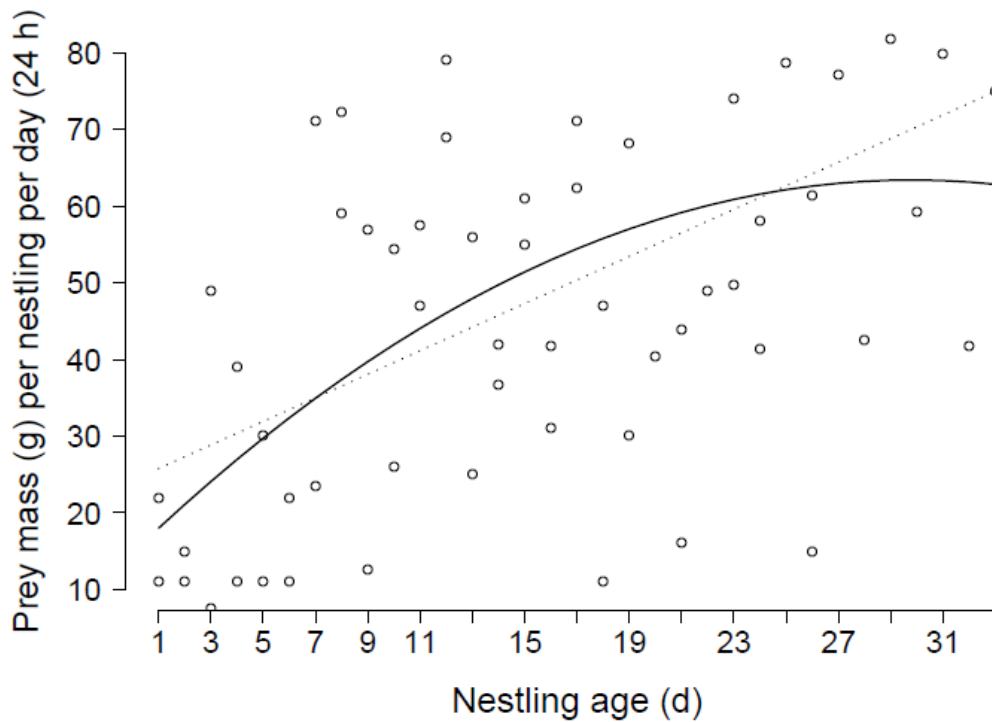
Figure 11: A linear and a non-linear model of prey mass (g) consumed per tawny owl nestling per day (24 h) as a function of nestling age (d), at two tawny owl nests (Hauger and Kroer).

Table 5: Parameter estimates from a linear model showing 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 = 59, random effect = 2 nests).

	Estimate	SE	t	p
Intercept	24.246	6.679	3.630	<0.001
Age	1.537	0.337	4.554	<0.001

Table 6: Parameter estimates from a non-linear model showing 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 = 59, random effect = 2 nests).

	Estimate	SE	t	p
Intercept	14.790	9.246	1.600	0.115
Age	3.264	1.286	2.538	0.014
I(Age^2)	-0.055	0.039	-1.409	0.164

There was no significant effect of the nestlings' age on the body mass of each prey item delivered (Table 7, 8). Thus, prey body mass was constant throughout the period, meaning it was the number of prey items that increased when the nestlings consumed more mass. Norderås was excluded from these tests.

Table 7: Parameter estimates from a linear model of prey body mass (g) as a function of nestling age (d). The model is corrected for nest ID (n = 333, random effect = 2 nests).

	Estimate	SE	t	p
Intercept	21.799	1.938	11.245	<0.001
Age	0.018	0.097	0.180	0.857

Table 8: Parameter estimates from a non-linear model of prey body mass (g) as a function of nestling age (d). The model is corrected for nest ID (n = 333, random effect = 2 nests).

	Estimate	SE	t	p
Intercept	22.225	3.402	6.533	<0.001
Age	-0.044	0.417	-0.105	0.917
$I(Age^2)$	0.002	0.012	0.152	0.879

4. Discussion

4.1 Diet composition

During the breeding season of 2017, the tawny owls I studied had a broad diet consisting of a wide variety of prey. In total, I recorded the delivery of 455 prey items, and of these 68.4 % were mammals, 12.3 % were birds, 4.6 % were amphibians, 0.2 % were reptiles (just one item), and 12.3 % were invertebrates (earthworms and insects). I was unable to identify 2.2 % of the prey. The estimated prey mass in percentage of identified prey were 76.2 % for mammals, 17.9 % for birds, 5.6 % for amphibians, 0.06 % for reptiles, and 0.2 % for invertebrates. The wood mouse was the prey species most often captured, with 20.4 % of all prey items. It was followed by different species of shrews (16.7 %), and then by bank vole (13.8 %), and field vole (7.9 %). Even if all the voles in the «bank vole or field vole» category had been field voles, the bank vole would still be more numerous than the field vole. There were also variations in the diet between the different locations.

My results are in agreement with previous findings in two main ways; the tawny owl is classified as a food generalist with a broad diet (e.g. Galeotti et al. 1991; Goszczynski et al. 1993; Zawadzka & Zawadzki 2007), and the tawny owl is able to adjust its diet based on the abundance of different prey species (Cramp 1985), which might be reflected by the differences in the diet composition between the three locations. In addition, rodents are considered as the most important part of the tawny owl diet (e.g., Capizzi 2000; Balčiauskiene et al. 2005; Zawadzka & Zawadzki 2007), which is also what I found at all the locations.

One interesting result in my study was the high percentage of wood mouse being delivered at the nest at Hauger (42.5 %). Petty (1999) found that the field vole was the most important prey for tawny owls in Northern England. Similarly, Obuch (2011) found the field vole to be the most common prey in Trøndelag, Norway. In other words then, even though the owls at Hauger showed a typical pattern with its amount of rodents compared to shrews, what I found differed from what might be exptected regarding which species of rodent is usually the most abundant. However, according to Luka & Riegert (2018) there is growing evidence to suggest that *Apodemus* mice and not *Microtus* or *Myodes* voles are the main prey of tawny owls, at least as observed in Central Europe. In addition to this, based on studies done similar to mine, what I found is what could be exptected from this particular location, Hauger. Results very similar to mine were obtained during breeding seasons prior to the one I studied; in 2015 the tawny owls at Hauger had a diet consisting of 58 % wood mouse (Stave 2015), and in 2016 the number was 38 % (Vik 2017). What I found, and what Stave and Vik also found, might be an example of tawny owls adjusting their diet to the abundance of different kind of prey species, demonstrating their generalist behaviour. Tawny owls are known for this ability; to take advantage of whatever suitable prey is available in a given location (Cramp 1985). The data from Hauger is also in line with the fact that snap trapping data in Ås for the spring of 2017 (Geir A. Sonerud, pers. comm) showed a relatively high abundance of wood mice. In other words, the results from this location may simply mean that what becomes the main prey for any particular breeding pair reflects different prey densities in he field, know as a functional response (Luka & Riegert 2018). This means that instead of either the field vole or the wood mice being the main prey of tawny owls, how these different species are represented in the diet of different tawny owls merely reflects their availability in the field (Opuch 2011).

Another interesting result was the high percentage of invertebrates delivered at the nest at Norderås. In a previous study, similar as mine, Sand (2016) found that the Norderås location had a very high percentage of invertebrates delivered to the nest compared to the other locations studied. Although my numbers (35.7 %) were not quite as high as Sand (2016) found (60 %), the pattern was still the same. Compared to the other two locations I studied, Hauger with 12.4 % invertebrate prey, and Kroer with 1.0 % invertebrate prey, Norderås stood out with a much higher percentage of invertebrate prey. It is not uncommon for invertebrates to be a part of the tawny owl diet, and even a percentage as high as 95 % has been reported (Manganaro et al. 2000). However, it does raise a few interesting possibilities.

One explanation of this high occurrence may be that there were fewer small mammals and rodents available at Norderås, forcing the tawny owls at this nest to catch more invertebrates. If this was the case, the same argument could be used as the one regarding wood mice, that the tawny owls adjusted their foraging behaviour to what was available. In other words, fewer available mammals meant they had to switch to a diet with more invertebrates. I have no data to suggest that this location had less mammals present, so I cannot conclude one way or another. Another possibility might be that instead of Norderås having fewer mammals available, it had more invertebrates available. Again, I cannot conclude whether or not this is the case, although this location has been described as an important insect biotope (Follorådet 1996 and references therein). But if it really is the case that there were more invertebrates available at Norderås than at the other locations, that leads to two different ways of answering the question of why the owls there captured so many invertebrates. Either it was random, that the owls simply preyed upon whatever they detected first, and invertebrates were readily available, so they just happened to catch these. Another possibility is that the tawny owls actually made a choice to hunt invertebrates over other prey. For example, insects, if they were abundant, would require little effort to catch, so were caught deliberately, to avoid what could have been a more time-consuming hunt. The owls would have to catch prey more frequently though, considering the low prey body mass of the invertebrates in question, but maybe the ease of the hunt made it profitable. In addition, invertebrates are easy for the nestlings to swallow, so the female parent would spend less time assisting the nestlings, and would be able to hunt instead (cf. Sonerud et al. 2014b). In other words, it might be an explanation that delivering invertebrates would be more profitable than delivering other prey, at this particular location. It would be very interesting for future studies to find ways to see if the relative abundance of mammals/rodents and invertebrates at this location is a factor in determining the diet of tawny owls at this nest.

4.2 Time of day of prey deliveries

Based on the probability of at least one prey delivery within an hour block, the tawny owls' main active period was within 20.00-03.59 with hunting activity peaking at 22.00-22.59. The peak had a value of 0.47. These results are consistent with the fact that the tawny owl is a nocturnal species (Cramp 1985). However, the value did not reach zero during daytime, and a few deliveries occurred even then. This has been reported to occur during the breeding season in previous studies of the tawny owl as well (Cramp 1985; Sand 2016, Vik 2017), and is most likely explained by the growing nestlings' need for food.

When comparing mammalian and avian prey, there was overall a higher probability of mammalian prey items being delivered than the probability of avian prey items being delivered within an hour block during the main activity period,. This is probably explained by both the fact that mammals, and small rodents in particular, are considered the main prey of tawny owls (e.g., Cramp 1985; Capizzi 2000), and the availability of rodents during nighttime. In my study, the wood mouse was the most delivered prey species. The fact that the wood

mouse is a nocturnal species (Flowerdew 2000), and that it is referred to as a monophasic species (Flowerdrew 2000), which means that it has an activity pattern with one long active phase, would make it readily available to tawny owls hunting at night. In addition to this, microtines and shrews would probably also be available at night, since they show an activity pattern called a polyphasic activity pattern (Halle 2000; Merrit & Vessey 2000), which means that they show an activity pattern with a short term rhythm, that switches between rest and active phases during both day and night. The difference in activity pattern between the different mammlian prey species, might also be part of the explaination why out of the mammals delivered at daytime at Kroer, 2 were wood mice, and 26 were shrews.

Overall, the probability of at least one avian prey delivery within an hour block was higher during the night than during the day, as it was for mammals, but the probability was much lower than for mammals. In addition, the peak value occurred later at night than for mammals, in the hour block 00.00-00.59, compared to mammals, where the peak occurred within the hour block 23.00-23.59. Both Sand (2016) and Vik (2017) also reported that the peak occurred later at night for avian prey than for mammals. The diel pattern in avian prey deliveries found in my study is also in accordance with the tawny owl being a nocturnal species (Cramp 1985), with more avian prey items being delivered during nightime than daytime, however, I cannot conclude as to why the peak occured later than for mammals. One possible explanation might relate to the importance of hearing when the tawny owls localize prey (Cramp 1985), and nighttime bird song. At least for thrushes in springtime, in my study area, it has been reported that they start singing a few minutes after solar midnight (Geir A. Sonerud pers. comm.) It therefore makes sense that it would be easier for tawny owls to capture these birds after they have started singing, delaying the peak in avian prey capture compared to mammals.

4.3 Prey handling in the nest

For any kind of prey, and for mammalian prey in particular, the probability of the nestlings feeding unassisted depended on both prey body mass and nestling age. The smaller the prey, and the older the nestlings, the higher was the probability that the nestlings fed unassisted. A similar pattern was found by Stave (2015), Sand (2016) and Vik (2017). Similarly, a study of nine raptor species (tawny owl not included) found that type and size of prey were important factors in determining when the female assisted the nestlings in feeding (Sonerud et al. 2014a). These results are are in line with the feeding constraint hypothesis (Slagsvold & Wiebe 2007), which states that the parents will evolve foraging and feeding behaviour adapted to assisting younger nestlings that are unable to ingest prey that older nestlings can manage. This predicts that the extent of prey preparation will increase with prey mass, and decrease with nestling age. Slagsvold & Wiebe (2007) studied prey preparation prior to delivery at the nest of passerines, with decapitation being an important factor. I found almost no evidence of decapitation, and very little evidence of other forms of prey preparation prior to delivery. So in my study, the relevant prey handling was whether or not the female parent

asssisted the nestlings in feeding, by dismembering the prey for them while in the nest. Nevertheless, the same principles applies; the larger the prey and the younger the nestlings, the more assistance from the female parent the nestlings required.

I found that the nestlings were in general most dependent on assistance from the female parent when avian prey were delivered to the nests. It has previously been reported that handling time in raptor species (not including the tawny owl) for avian prey when nestlings fed unassisted was more time consuming (Sonerud et al. 2014a,b), so it is recognized that birds can pose a challenge to nestlings. It makes sense that the shape of the prey determines the ease at which a nestling will be able to ingest the item, and that items are smoother, and have less protrubing appendages, are easier for nestlings to consume without parental assistance. Løw (2006) reported that even when avian prey were plucked prior too delivery at kestrel nests, they were still the prey that were the most difficult to handle for the nestlings, based on results of frequency of unassisted feeding, which was low, the high age at which the switch occurred, and the long handling time. These previous findings are in line with my results, regarding the difference in frequency of unassisted feeding of birds compared to mammals.

3.4 Prey mass delivered

Both the linear and non-linear models describing prey mass delivered as a function of nestling age in my study, showed an increase in prey mass (g) per nestling per day (24 h) throughout the entire observational period, which lasted until all the nestlings from all the nest boxes had fledged. In other words, more and more prey mass was delivered per nestling per day even up until the point they left the nest.

The increase in prey mass delivered as the nestlings grew older is in accordance with previous research that states that the demand for food increases with age. Since growth rate is not constant, the nestlings need for energy might also increase with an increased growth rate (Barba et al. 2009; Steen et al. 2012). The increase in prey mass delivered might therefore be a result of the parents adjusting their food provisioning to the energy demands of the nestlings. The interesting aspect of the results from the tawny owl nests I studied, is the linear trend up to fledging, i.e. there was a continuous increase in prey mass delivered, and never a point where a peak occurred, followed by a decrease. A differing pattern from what I found has previously been reported for passerines; that there is usually an increase in feeding rates with nestling age, and that this is followed by a decrease as the maximum body mass of the nestlings is approached (Grundel 1987; Blondel et al. 1991; Barba et al. 2009). This is also what Steen et al. (2012) found for the Eurasian kestrel (*Falco tinnunculus*); a non-linear relationship shaped like an inverted U, between prey mass delivered per nestling per day and nestling age. No such trend was found in my study, but I cannot conclude that such an effect would not have occurred, had I continued to monitor prey deliveries after the nestlings fledged. Southern et al. (1954) found that in the period of 2.5-3 months after fledging, young tawny owls made no effort to feed themselves, instead the parents continued to provide food for them. It would be be interesting to see if the linear trend continued after fledging of the

nestlings in my study, or if there would be a decrease in prey mass delivered. According to Cramp (1985), tawny owls feeding rate is at its greatest at the age of 11-25 days. Based on that, one could assume that the greatest food demand for nestlings would be when they are still inside the nest box, and that therefore there would be a decrease after fledging, but I have no data to support this either way.

5. Conclusion

My study showed that the tawny owls utilised a broad diet, consisting of mammals, birds, amphibians, reptiles, earthworms and insects, and that the tawny owls were mostly active during nighttime. This is in line with previous research, thereby confirming the tawny owl to be a food generalist and a nocturnal species. The probability of nestlings feeding unassisted was dependent on prey mass and nestling age for mammalian prey, but only on nestling age for avian prey. Also, that the probability of ingesting birds unassisted never reached as high values as for ingesting mammals unassisted, which is in accordance with previous findings that have showed that nestlings generally have more difficulties with avian prey items than other prey items. Finally, prey body mass did not increase with nestling age, meaning that more prey items were delivered to the nests when the nestlings consumed more prey mass, instead of larger prey items being delivered.

6. References

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Appendix

Appendix 1: Nature, red in tooth and claw.

Appendix 2: Parameter estimates from the model showing the probability of at least one prey delivery per hour block (n = 2086, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.240	0.220	-10.185	<0.001
I(cos(2 * pi * Hour/24))	1.830	0.132	13.842	<0.001
I(sin(2 * pi * Hour/24))	0.170	0.149	1.136	0.256
I(cos(2 * 2 * pi * Hour/24))	0.671	0.134	5.005	<0.001
I(sin(2 * 2 * pi * Hour/24))	0.091	0.147	0.621	0.535
I(cos(3 * 2 * pi * Hour/24))	-0.370	0.120	-3.070	0.002
I(sin(3 * 2 pi * Hour/24))	-0.239	0.117	-2.032	0.042

Appendix 3: Parameter estimates from the model showing the probability of at least one mammalian prey delivery per hour block (n = 2086, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.715	0.196	-13.873	<0.001
I(cos(2 * pi * Hour/24))	1.887	0.165	11.429	<0.001
I(sin(2 * pi * Hour/24))	-0.080	0.182	-0.437	0.662
I(cos(2 * 2 * pi * Hour/24))	0.652	0.160	4.065	<0.001
I(sin(2 * 2 * pi * Hour/24))	0.271	0.184	1.474	0.140
I(cos(3 * 2 * pi * Hour/24))	-0.391	0.140	-2.795	0.005
I(sin(3 * 2 pi * Hour/24))	-0.320	0.138	-2.303	0.021

Appendix 4: Parameter estimates from the model showing the probability of at least one avian prey delivery per hour block (n = 2086, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-4.443	0.272	-16.35	<0.001
I(cos(2 * pi * Hour/24))	2.017	0.337	5.993	<0.001
I(sin(2 * pi * Hour/24))	0.341	0.236	1.447	0.148