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Diet, diel activity and prey handling in the tawny owl (*Strix aluco*), as revealed by video monitoring of prey deliveries at the nest

Diett, døgnaktivitet og byttedyr-
handtering hos kattugle (*Strix aluco*)
observert ved videoovervåking av
byttedyrleveringer på reiret

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Master in Management of Natural Resources

Acknowledgements

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Abstract

Prey deliveries and prey handling at three nests of the tawny owl (*Strix aluco*) in Akershus county in Norway were video monitored during the nesting period. In total, 712 prey items were recorded, and 619 of these were identified to species or higher taxa. Vertebrates made up 50.7 % of all prey items by number and 92.5 % by mass, while invertebrates made up 36.2 % by number and 0.9 % by mass. Mammals were the most important prey group (32.6 % by number and 56.8 % by mass), followed by birds (15.0 % by number and 30.2 % by mass), amphibians (2.0 % by number and 4.3 % by mass) and reptiles (1.1 % by number and 1.2 % by mass). The remaining percentages were unidentified prey items. The prey deliveries happened mostly during the night, with the highest probability of at least one prey delivery per hour block between 00:00 and 01:00. As the nestlings grew older, they were more likely to ingest prey items unassisted. Smaller prey items did also increase the probability of the nestlings feeding unassisted. The amount of prey mass consumed per nestling per day increased with both nestling age and season, i.e. number of days elapsed after the video monitoring started.

Sammendrag

Byttedyrleveringer og byttedyrhandtering på tre reir av kattugle (*Strix aluco*) i Akershus fylke i Norge ble videoovervåket i hekkesesongen. Totalt ble 712 byttedyr registrert, og 619 av disse ble identifisert til art eller høyere klassifisering. Vertebrater utgjorde 50,7 % av alle byttedyrene i antall og 92,5 % i vekt, mens evertebrater utgjorde 36,2 % i antall og 0,9 % i vekt. Pattedyr var den viktigste byttedyrgruppa (32,6 % i antall og 56,8 % i vekt), etterfulgt av fugler (15,0 % i antall og 30,2 % i vekt), amfibier (2,0 % i antall og 4,3 % i vekt) og reptiler (1,1 % i antall og 1,2 % i vekt). De resterende prosentandelene var uidentifiserte byttedyr. Byttedyrleveringene skjedde for det meste om natta, med den høyeste sannsynligheten for minst en byttedyrlevering pr timesblokk mellom kl.00.00 og kl.01.00. Ettersom ungene ble eldre, økte sannsynligheten for at de spiste på egen hånd. Små byttedyr økte også sannsynligheten for at ungene spiste på egen hånd. Andelen byttedyrmasse som ble konsumert pr unge pr dag økte med både alder til ungene og sesong, dvs. antall dager som hadde gått etter at videoovervåkingsperioden startet.

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1. Introduction

Raptors (i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes)) are well studied and a lot is known about their ecology, including their diet, diel activity and prey handling (Cramp & Simmons 1980; Cramp 1985). What is known about raptors' choice of prey is, however, mostly based upon analysis of pellets and other remains of prey found at nest sites (e.g. Cramp 1985; Slagsvold et al. 2010). Using only pellets and remains of prey might give a biased estimate of the diet of raptors and probably overestimate the amount of large prey and birds in the diet (Slagsvold et al. 2010). Video monitoring of prey deliveries at the nest will therefore most likely give a more accurate estimate of the diet by recording all prey delivered at the nests during the video monitoring period.

Since video monitoring makes it possible to monitor raptor nests continuously throughout both day and night, it can be used to study the activity patterns of raptors in relation to environmental factors. Many animals show specific activity rhythms related to day and night, and also to season, which affect the ecology and behaviour of the species (Erkert & Kappeler 2004). Animals that exhibit a particular activity pattern, e.g. a diurnal activity pattern or a nocturnal activity pattern, might show certain anatomical, physiological and behavioural adaptations to their way of living (Kronfeld-Schor & Dayan 2003). These adaptations are most likely a result of many factors, e.g. the activity patterns of both congeners and individuals of other species, which can create intraspecific and interspecific competition, as well as the activity pattern of prey, predators and parasites (Mistlberger & Skene 2004). Raptors, and also small mammals, which are the main prey of many raptors, exhibit specific activity patterns (Cramp & Simmons 1980; Cramp 1985; Halle & Stenseth 2000). Some raptors show a nocturnal or diurnal activity pattern, while others are active also at twilight (Cramp & Simmons 1980; Jaksić 1982; Cramp 1985). The activity pattern of raptors may be closely related to when their prey species are available, as well as what kind of hunting strategy they have developed. Raptors that hunt by sight are restricted to hunting in daylight, while raptors that hunt by hearing can also hunt at night (Newton 1979; Cramp & Simmons 1980; Cramp 1985).

Video monitoring at nests can also give important information regarding prey handling in raptors. The female, which is typically larger than the male, broods and assists the nestlings

during feeding (Newton 1979; Sonerud et al. 2013). The male provides prey, which the female allocates between herself and the nestlings (Sonerud et al. 2013). When the nestlings are young, they are dependent on the female for preparation of large prey items, and therefore the female will be confined to the nest in the first part of the nestling period (Sonerud et al. 2013). In the latter part, the female might assist the male with food provisioning (Sonerud et al. 2013). The degree of assistance needed in prey preparation varies with size and type of prey (Sonerud et al. 2014a).

One raptor that has been the object of numerous studies throughout the years is the tawny owl (*Strix aluco*), the most common owl in Europe (Zawadzka & Zawadzki 2007). The tawny owl is a medium sized, resident and territorial owl found throughout the Palearctic region (Cramp 1985; Jędrzejewski et al. 1996). It is common in the lowlands of eastern Norway and in the coastal areas of Norway as far north as Trøndelag (Sonerud 1994). As most owls, the tawny owl is nocturnal and captures prey that are available at night (Cramp 1985). When hunting, it mostly uses look-out posts and a sit-and-wait tactic (Southern 1954; Redpath 1995), but hunting in flight has also been reported (Nilsson 1978). The hearing is well developed in the tawny owl and is important when localizing prey during hunting (Cramp 1985). The tawny owl is often defined as a food generalist because it catches many different types of prey (e.g. Galeotti 1990; Galeotti et al. 1991; Goszczynski et al. 1993; Sunde et al. 2001; Zawadzka & Zawadzki 2007), including mammals, birds, amphibians, earthworms and beetles, depending on what is available at a given place and time (Cramp 1985). This probably makes the tawny owl highly adaptable to natural fluctuations in prey species density, though the breeding success of the tawny owl has been reported to vary according to the availability of small mammals (Karell et al. 2009).

I have studied the diet, diel activity and prey handling in tawny owls by video monitoring prey deliveries at nests during the breeding season of 2015. A study of prey deliveries at four nests of the tawny owl was conducted in Akershus county in 2014, which was a small rodent peak year (Stave 2015). In contrast was 2015 expected to be a year with relatively few rodents, and I wanted to see if and how the diet of tawny owls in the same area would change. I hypothesized that the diet of tawny owls would change and that it would consist of a larger proportion of alternative prey species, for instance birds and amphibians (Jędrzejewski et al. 1996). My main goals were to find out i) what prey are delivered at nests of the tawny owl, ii)

at what time of the day do the prey deliveries happen, iii) what influences whether the female feeds her nestlings rather than the nestlings ingest the prey themselves, and iv) the amount of prey that the nestlings consume.

2. Methods

2.1 Study area

The study was conducted in Ås and Vestby municipalities in Akershus county (59°38'N, 10°45'E) during the spring and early summer of 2015. Three nests of the tawny owl were chosen, all in nest boxes. One of the nest boxes was located in Vestby (location Ramme), while the other two nest boxes were located in Ås (locations Norderås and Kroer) with a distance of c. 10 km between the boxes (Figure 1). The nest box at Norderås was located in a small patch of deciduous forest surrounded by fields to the west and south, and forest to the east and north. The nest box at Kroer was located at the border between a field and a large area of coniferous forest. The nest box at Ramme was located close to an area with both deciduous and coniferous forest. The nest box at Ramme was also located in close proximity to the Oslo fjord, in an area with a number of holiday cabins.

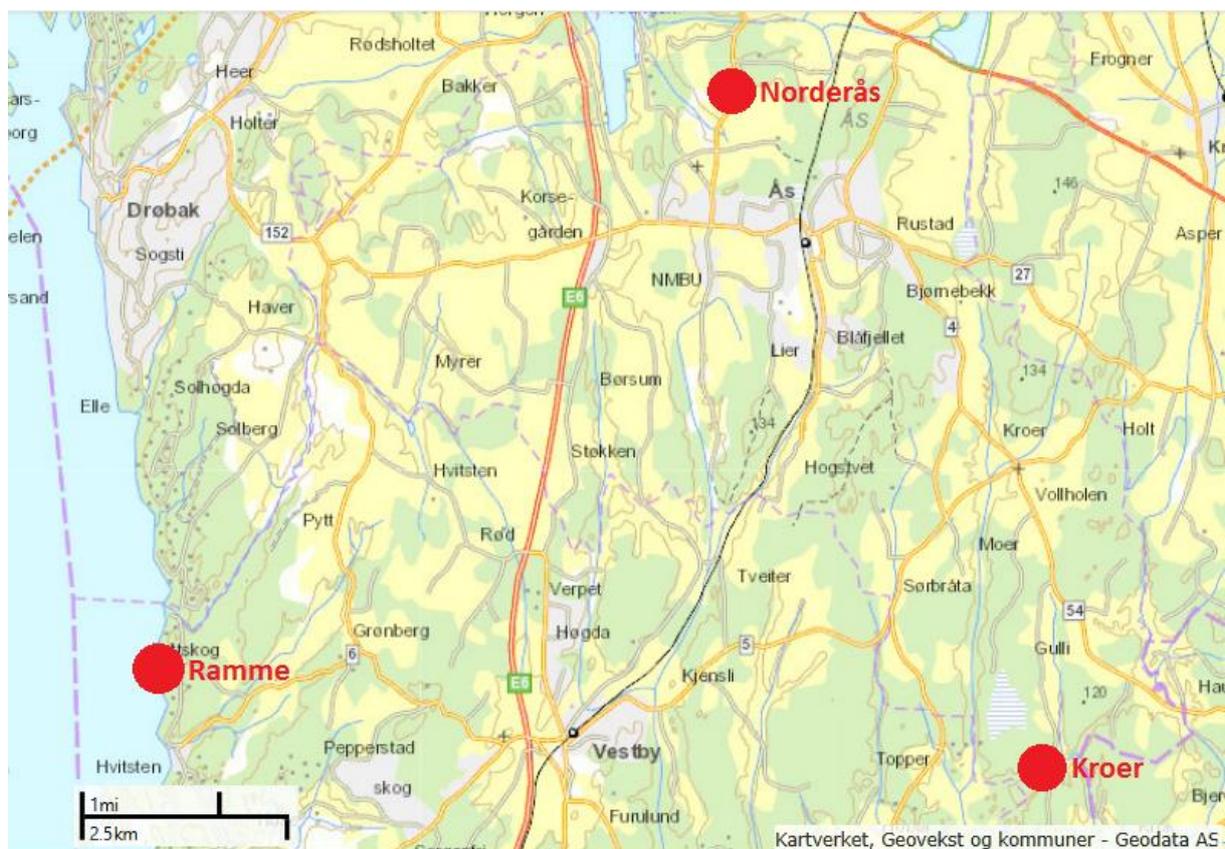


Figure 1: The study area with the three tawny owl nest box locations (Norderås, Kroer and Ramme) marked with red dots.

2.2 Video monitoring

I used a modification of the study design described by Steen (2009) to monitor the nests. A camera was installed inside each nest box, a wide angle lens was used to both cover the entrance and most of the area inside (Appendix 1). At two of the nest locations (Kroer and Ramme) the camera was installed before the nestlings had hatched, but at the third nest location (Norderås) the camera was installed when the nestlings were about five days old. At each nest the camera used was a mini charge-coupled device (CCD) camera with infrared light, making it possible to record in poor light conditions. The camera was connected by a cable to a mini digital video recorder (DVR) where the recordings were saved on 32 GB SD cards. The mini DVRs used were Secumate H.264 Mini Portable DVRs. At two of the nest locations (Kroer and Norderås) 12V 80AH batteries were also installed together with the mini DVRs approximately 20 m from the nest boxes to avoid disturbance when changing SD cards and batteries. The video equipment at the third nest location (Ramme) was powered from the local grid. Video motion detection (VMD) was used to avoid continuous recording. VMD enables event recording, triggered by moving objects within the camera's fixed field because of changes recorded in successive images. All except the entrance of the nest box was digitally masked, this prevented nestlings to trigger the video recording, and only being triggered by parents entering or leaving the nest box (see Steen (2009) for further details). I used 5 seconds pre-recording and 10 second post-recording after a trigger. With the pre-recording, the video is buffered continuously and 5 seconds prior to the trigger is kept. This to make sure that no important footage in connection with prey deliveries and feeding would be lost.

2.3 Video analysis

A total of 302 hours and 47 minutes of video clips were recorded during the monitoring period. The video clips varied in length from a few seconds to about fifteen minutes. All video clips were looked through, and those showing prey deliveries were separated from the rest of the recordings. I made a closer video analysis of these video clips together with Geir A. Sonerud and Vidar Selås, and the prey items were identified to the best of our ability. The identification of prey was based on body size, coloration, fur structure, head shape, ear size, tail length, eye size, beak shape and size, plumage and overall appearance, depending on the type of prey. When identification to species was not possible, identification was restricted to

prey group (e.g. Cricetidae, Rodentia or Mammalia). Some prey items were not possible to identify.

I have chosen not to specify shrews (Soricidae) or frogs (*Rana sp.*) to species. Most of the shrews were believed to be common shrew (*Sorex araneus*), but we could not rule out the possibility that some of the shrews were Eurasian water shrews (*Neomys fodiens*) or Eurasian pygmy shrews (*Sorex minutus*). Most of the frogs were believed to be common frogs (*Rana temporaria*), but we could not rule out the possibility that some of them were moor frogs (*Rana arvalis*). All prey identified as *Apodemus sp.* were registered as wood mice (*Apodemus sylvaticus*), since this is the only *Apodemus* species that has been caught in an annual snap trapping program at Ås during spring from 1993 to 2015 (Geir A. Sonerud, pers. comm.).

The date and time of when the owl landed at the box entrance with prey was registered for each prey delivery by viewing the time stamp at the footage. In addition, whether the nestlings ingested the prey unassisted or were fed by the female was registered, as well as the nestlings' age at that time. Nestling age was defined as the age of the youngest nestling in each brood.

2.4 Estimation of prey body mass

Estimated prey body mass of mammalian species were obtained from data on snap trapping at Ås from 1993 to 2015 (Geir A. Sonerud, pers. comm.). Unidentified voles were given an estimated body mass based on the number of each species of identified voles for each nest. The same was done with unidentified rodents and unidentified mammals. Since bird body mass has relatively small intraspecific variation, a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp 1988, 1992; Cramp & Perrins 1993, 1994; Selås 2001). For passerines, juveniles were assigned the same body mass as adults. Reptiles and frogs were given estimates the same way as was done for mammals (Vidar Selås and Geir A. Sonerud, pers. comm.). Frogs were in addition divided into two groups (small and large) which were given separate body mass estimates based on how large they appeared on the video screen. The body mass of earthworms was taken from Stave (2015). The body mass of insects was taken from Itämies and Korpimäki (1987). Because the unidentified invertebrates were believed to be as small as insects, they were given

the same estimated body mass as the insects. Unidentified prey items were given an estimated body mass based on the number of all the other prey items in each nest.

2.5 Statistical analysis

Statistical analysis of the data was done using the software programs R version 3.1.2 (R Development Core Team 2014) and JMP Pro version 12.1.0 (SAS Institute Inc. 2015). JMP Pro version 12.1.0 was initially used to get an overview of the data and to calculate percentages, but for the more advanced statistical analysis R version 3.1.2 was used. The only exception was that JMP Pro version 12.1.0 was used to calculate the mean estimated prey body mass of all prey items by setting the estimated prey mass as the response variable and including no other effects than the random effect of nest ID. Figures 2-5 were constructed with SigmaPlot version 11.0 (Systat Software Inc. 2008), while Figure 6 and Figure 7 were constructed with Microsoft Excel. In R version 3.1.2 the packages “nlme” (Pinheiro et al. 2014) and “lme4” (Bates et al. 2014) were used to perform mixed-effect regression models. Both linear and logistic regression models were used.

To analyse the circadian activity rhythm of the tawny owl, the periodic components of time series were set as sine and cosine functions (Pita et al. 2011). All 24 hour periods were divided into hour blocks from 0 to 24, which were used as the sample unit. The response variable was the probability of at least one prey delivery within a certain hour block. An hour block with at least one prey delivery was scored as “yes”, while hour blocks without any prey deliveries were scored as “no”. In the equations that were used for the activity models, the different hour blocks were expressed as x , while the random effect, expressed as ε , was a correction for nest ID. The models were also assessed according to AIC values (Burnham & Anderson 2002). The models (M_1 - M_4) were as follows:

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

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

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

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

$$\left(a_3 \cos \frac{3 \cdot 2\pi x}{24} + b_3 \sin \frac{3 \cdot 2\pi x}{24} \right) + \varepsilon$$

In the test on prey handling in the nest the probability of the nestlings feeding unassisted was the response variable, while nestling age and estimated prey mass were explanatory variables. Models including only one of the explanatory variables were made, as well as a model including both. All models were corrected for nest ID. The models were assessed according to AIC values (Burnham & Anderson 2002). Calculations were also made to find out when the probability of the nestlings ingesting the prey unassisted was the same as the probability of the female assisting them.

Finally, whether prey mass consumed by the nestlings changed throughout the monitoring period was tested. In this test the response variable was prey mass consumed per nestling per day. As explanatory variables, both nestling age and season (defined as the number of days after the monitoring period started) were used. The explanatory variables were highly correlated, and were therefore used in separate models. The models were corrected for nest ID, and assessed according to AIC values (Burnham & Anderson 2002). When calculating prey mass consumed per nestling per day, days that had not been monitored for 24 hours was omitted, as well as deliveries of prey that were not consumed by the nestlings.

3. Results

3.1 Composition of the diet

The tawny owls had a diverse diet (Table 1). I registered 712 prey items in total at the three nest locations. Mean estimated prey body mass were 22.9 ± 1.3 g for nest location Kroer, 17.1 ± 1.1 g for nest location Ramme and 5.1 ± 0.5 g for nest location Norderås. The mean estimated prey body mass in total was 15.0 ± 5.2 g (corrected for nest ID). By number, identified vertebrates made up 50.7 % of all prey items, while identified invertebrates made up 36.2 %. The remaining 13.1 % were unidentified prey. Thus, among identified prey item, vertebrates made up 58.3 % and invertebrates 41.7 %. Even though slightly more than half of the prey items were vertebrates, they made up almost all the estimated total prey mass (at least 92.5 %). Invertebrates made up at least 0.9 % of the estimated total prey mass, while unidentified prey made up 6.5 % of the estimated total prey mass. Thus, among identified prey, vertebrates made up 99.0 % of the delivered prey mass, and invertebrates 1.0 %.

Vertebrates delivered at the tawny owls' nests included mammals, birds, amphibians and reptiles, while invertebrates included insects and earthworms. By number mammals made up the highest percentage of all prey delivered both by number (32.6 %) and by estimated prey mass (56.8 %) (Table 1, Table 2). Shrews were the most numerous mammalian prey delivered at the nests (Table 1), but field voles (*Microtus agrestis*), wood mice and bank voles (*Myodes glareolus*) each made up >5 % of prey by number, and >10 % of the estimated total prey mass (Table 1, Table 2).

Table 1: Number of prey items delivered at three tawny owl nests (Kroer, Ramme and Norderås) during the breeding season of 2015, with percentages by number of prey items for each nest, as well as in total.

Species	Kroer		Ramme		Norderås		Total	
	No.	%	No.	%	No.	%	No.	%
Least weasel (<i>Mustela nivalis</i>)	1	0.6	0	0.0	0	0.0	1	0.1
Shrew (<i>Sorex araneus</i> , <i>Neomys fodiens</i> or <i>Sorex minutus</i>)	33	19.3	31	17.5	4	1.1	68	9.6
Field vole (<i>Microtus agrestis</i>)	28	16.4	14	7.9	0	0.0	42	5.9
Bank vole (<i>Myodes glareolus</i>)	18	10.5	21	11.9	7	1.9	46	6.5
European water vole (<i>Arvicola amphibious</i>)	0	0.0	1	0.6	0	0.0	1	0.1
Unidentified vole (Cricetidae)	3	1.8	7	4.0	5	1.4	15	2.1
Wood mouse (<i>Apodemus sylvaticus</i>)	3	1.8	32	18.1	6	1.6	41	5.8
Unidentified small rodent	1	0.6	2	1.1	8	2.2	11	1.5
Unidentified small mammal	0	0.0	2	1.1	5	1.4	7	1.0
Mammals total	87	50.9	110	62.1	35	9.6	232	32.6
European robin (<i>Erithacus rubecula</i>)	3	1.8	0	0.0	0	0.0	3	0.4
Whinchat (<i>Saxicola rubetra</i>)	2	1.2	0	0.0	0	0.0	2	0.3
Red-backed shrike (<i>Lanius collurio</i>)	0	0.0	0	0.0	1	0.3	1	0.1
Song thrush (<i>Turdus philomelos</i>)	6	3.5	0	0.0	1	0.3	7	1.0
Fieldfare (<i>Turdus pilaris</i>)	0	0.0	1	0.6	0	0.0	1	0.1
Unidentified thrush (<i>Turdus sp.</i>)	13	7.6	1	0.6	2	0.5	16	2.2
Common chiffchaff (<i>Phylloscopus collybita</i>)	1	0.6	0	0.0	0	0.0	1	0.1
Willow warbler (<i>Phylloscopus trochilus</i>)	0	0.0	1	0.6	1	0.3	2	0.3
Unidentified warbler (Sylviidae)	0	0.0	1	0.6	0	0.0	1	0.1
White wagtail (<i>Motacilla alba</i>)	0	0.0	1	0.6	0	0.0	1	0.1
Great tit (<i>Parus major</i>)	0	0.0	0	0.0	1	0.3	1	0.1
Willow tit (<i>Poecile montanus</i>)	1	0.6	0	0.0	0	0.0	1	0.1
Unidentified tit (Paridae)	1	0.6	1	0.6	0	0.0	2	0.3
Common chaffinch (<i>Fringilla coelebs</i>)	5	2.9	0	0.0	2	0.5	7	1.0
Eurasian siskin (<i>Carduelis spinus</i>)	0	0.0	1	0.6	0	0.0	1	0.1
Unidentified small bird	33	19.3	11	6.2	15	4.1	59	8.3
Unidentified bird	0	0.0	0	0.0	1	0.3	1	0.1
Birds total	65	38.0	18	10.2	24	6.6	107	15.0
Slow worm (<i>Anguis fragilis</i>)	1	0.6	6	3.4	0	0.0	7	1.0
Common lizard (<i>Zootoca vivipara</i>)	1	0.6	0	0.0	0	0.0	1	0.1
Reptiles total	2	1.2	6	3.4	0	0.0	8	1.1
Frog (<i>Rana sp.</i>)	11	6.4	0	0.0	3	0.8	14	2.0
Amphibians total	11	6.4	0	0.0	3	0.8	14	2.0
Earthworm (Lumbricidae)	4	2.3	12	6.8	33	9.1	49	6.9
Common cockchafer (<i>Melolontha hippocastani</i>)	0	0.0	5	2.8	0	0.0	5	0.7
Unidentified earth-boring dung beetle (Geotrupidae)	0	0.0	1	0.6	0	0.0	1	0.1
Unidentified beetle (Coleoptera)	0	0.0	2	1.1	0	0.0	2	0.3
Unidentified owl moth (Noctuidae)	1	0.6	0	0.0	0	0.0	1	0.1
Unidentified Lepidoptera larvae	0	0.0	1	0.6	0	0.0	1	0.1
Unidentified insect larvae	0	0.0	9	5.1	81	22.3	90	12.6
Unidentified small invertebrate	0	0.0	6	3.4	103	28.3	109	15.3
Invertebrates total	5	2.9	36	20.3	217	59.6	258	36.2
Unidentified prey	1	0.6	7	4.0	85	23.4	93	13.1
All prey total	171	100.0	177	100.0	364	100.0	712	100.0

Table 2: Estimated prey body mass (g) delivered at three tawny owl nests (Kroer, Ramme and Norderås) during the breeding season of 2015, with percentages by prey mass for each nest, as well as in total.

Species	Kroer		Ramme		Norderås		Total	
	g	%	g	%	g	%	g	%
Least weasel (<i>Mustela nivalis</i>)	40	1.0	0	0.0	0	0.0	40	0.5
Shrew (<i>Sorex araneus</i> , <i>Neomys fodiens</i> or <i>Sorex minutus</i>)	330	8.4	310	10.7	40	2.1	680	7.7
Field vole (<i>Microtus agrestis</i>)	896	22.9	448	14.8	0	0.0	1344	15.3
Bank vole (<i>Myodes glareolus</i>)	396	10.1	462	15.3	154	8.2	1012	11.5
European water vole (<i>Arvicola amphibious</i>)	0	0.0	100	3.3	0	0.0	100	1.1
Unidentified vole (Cricetidae)	84.3	2.2	185.6	6.1	110	5.9	379.9	4.3
Wood mouse (<i>Apodemus sylvaticus</i>)	75	1.9	800	26.5	150	8.0	1025	11.6
Unidentified small rodent	27.9	0.7	53.2	1.8	184	9.8	265.1	3.0
Unidentified small mammal	0	0.0	43.6	1.4	106.5	5.7	150.1	1.7
Mammals total	1849.2	47.3	2402.4	79.6	744.5	39.8	4996.1	56.8
European robin (<i>Erithacus rubecula</i>)	54	1.4	0	0.0	0	0.0	54	0.6
Whinchat (<i>Saxicola rubetra</i>)	32	0.8	0	0.0	0	0.0	32	0.4
Red-backed shrike (<i>Lanius collurio</i>)	0	0.0	0	0.0	28	1.5	28	0.3
Song thrush (<i>Turdus philomelos</i>)	384	9.8	0	0.0	74	4.0	458	5.2
Fieldfare (<i>Turdus pilaris</i>)	0	0.0	105	3.5	0	0.0	105	1.2
Unidentified thrush (<i>Turdus sp.</i>)	745	19.0	80	2.6	120	6.4	945	10.7
Common chiffchaff (<i>Phylloscopus collybita</i>)	9	0.2	0	0.0	0	0.0	9	0.1
Willow warbler (<i>Phylloscopus trochilus</i>)	0	0.0	9	0.3	9	0.5	18	0.2
Unidentified warbler (Sylviidae)	0	0.0	10	0.3	0	0.0	10	0.1
White wagtail (<i>Motacilla alba</i>)	0	0.0	21	0.7	0	0.0	21	0.2
Great tit (<i>Parus major</i>)	0	0.0	0	0.0	18	1.0	18	0.2
Willow tit (<i>Poecile montanus</i>)	12	0.3	0	0.0	0	0.0	12	0.1
Unidentified tit (Paridae)	12	0.3	12	0.4	0	0.0	24	0.3
Common chaffinch (<i>Fringilla coelebs</i>)	115	2.9	0	0.0	46	2.5	161	1.8
Eurasian siskin (<i>Carduelis spinus</i>)	0	0.0	11	0.4	0	0.0	11	0.1
Unidentified small bird	364	9.3	145	4.8	220	11.8	729	8.3
Unidentified bird	0	0.0	0	0.0	22.4	1.2	22.4	0.3
Birds total	1727	44.1	393	13.0	537.4	28.8	2657.4	30.2
Slow worm (<i>Anguis fragilis</i>)	15	0.4	90	3.0	0	0.0	105	1.2
Common lizard (<i>Zootoca vivipara</i>)	5	0.1	0	0.0	0	0.0	5	<0.1
Reptiles total	20	0.5	90	3.0	0	0.0	110	1.2
Frog (<i>Rana sp.</i>)	290	7.4	0	0.0	90	4.8	380	4.3
Amphibians total	290	7.4	0	0.0	90	4.8	380	4.3
Earthworm (Lumbricidae)	3.2	0.1	9.6	0.3	26.4	1.4	39.2	0.4
Common cockchafer (<i>Melolontha hippocastani</i>)	0	0.0	1	<0.1	0	0.0	1	<0.1
Unidentified earth-boring dung beetle (Geotrupidae)	0	0.0	0.2	<0.1	0	0.0	0.2	<0.1
Unidentified beetle (Coleoptera)	0	0.0	0.4	<0.1	0	0.0	0.4	<0.1
Unidentified owl moth (Noctuidae)	0.2	<0.1	0	0.0	0	0.0	0.2	<0.1
Unidentified Lepidoptera larvae	0	0.0	0.2	<0.1	0	0.0	0.2	<0.1
Unidentified insect larvae	0	0.0	1.8	0.1	16.2	0.9	18	0.2
Unidentified small invertebrate	0	0.0	1.2	<0.1	20.6	1.1	21.8	0.2
Invertebrates total	3.4	0.1	14.4	0.5	63.2	3.4	81	0.9
Unidentified prey	22.9	0.6	119.7	4.0	433.5	23.2	576.1	6.5
All prey total	3912.5	100.0	3019.5	100.0	1868.6	100.0	8800.6	100.0

3.2 Time of day of prey deliveries

The probability of at least one prey delivery per hour block was higher during the night than during the day (Figure 2, Appendix 2). This probability peaked at the hour block lasting from 00:00 to 01:00 with a value of 0.53. The average activity of the tawny owls, as indicated from the model with only the random effect included, was 0.17 (i.e. the midline estimating statistic of rhythm - MESOR). Probabilities of prey delivery higher than 0.17 were therefore considered as indicating that the tawny owls were active and hunting (main activity period), which corresponded to the period between 21:00 and 05:00 (Figure 2).

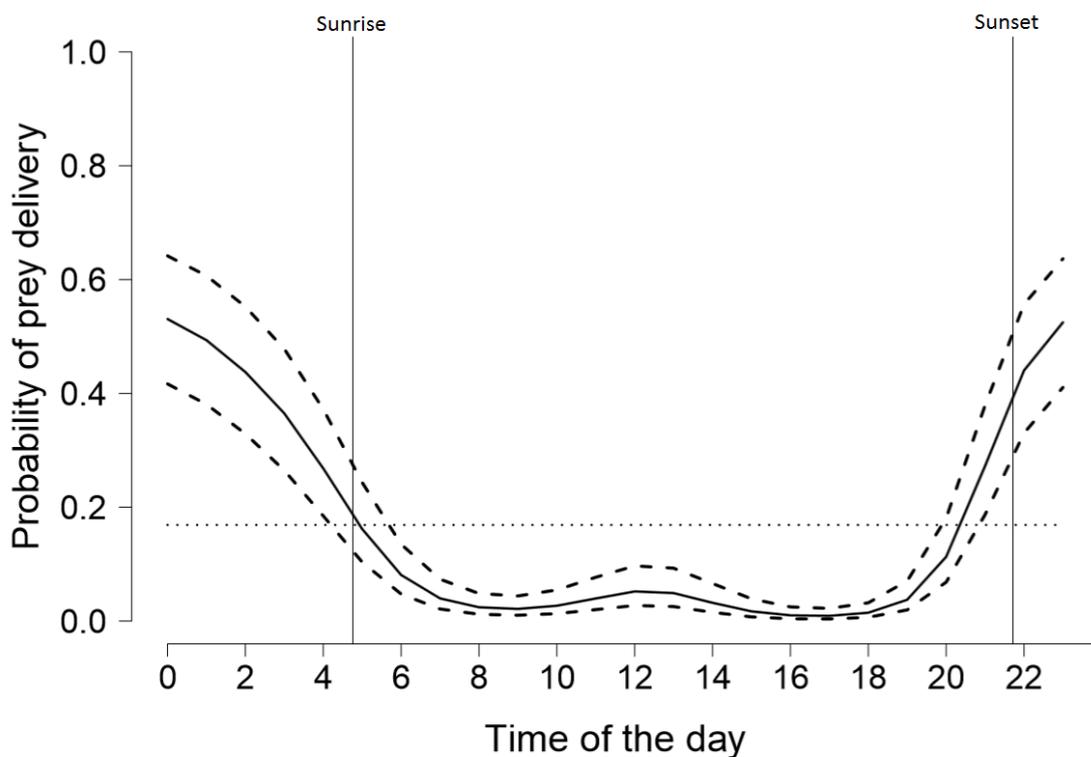


Figure 2: Probability of at least one prey delivery per hour block at tawny owl nests as a function of time of day (h), predicted from models of circadian activity rhythms. The two dashed lines represent the confidence interval, while the dotted line is the midline estimating statistic of rhythm (MESOR).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

The probability of at least one prey delivery per hour block was overall higher for mammalian prey than for avian prey (Figure 3, Appendices 3 and 4). The probability of at least one

delivery of a mammalian prey peaked at the hour block lasting from 00:00 to 01:00, with a value of 0.30, while the corresponding estimate for avian prey peaked at the hour block lasting from 01:00 to 02:00, with a value of 0.12. The time at which the probability of prey delivery became higher than average in the evening and below average in the morning (i.e. above and below MESOR, respectively), was delayed by one hour block for avian prey compared to mammalian prey (Figure 3).

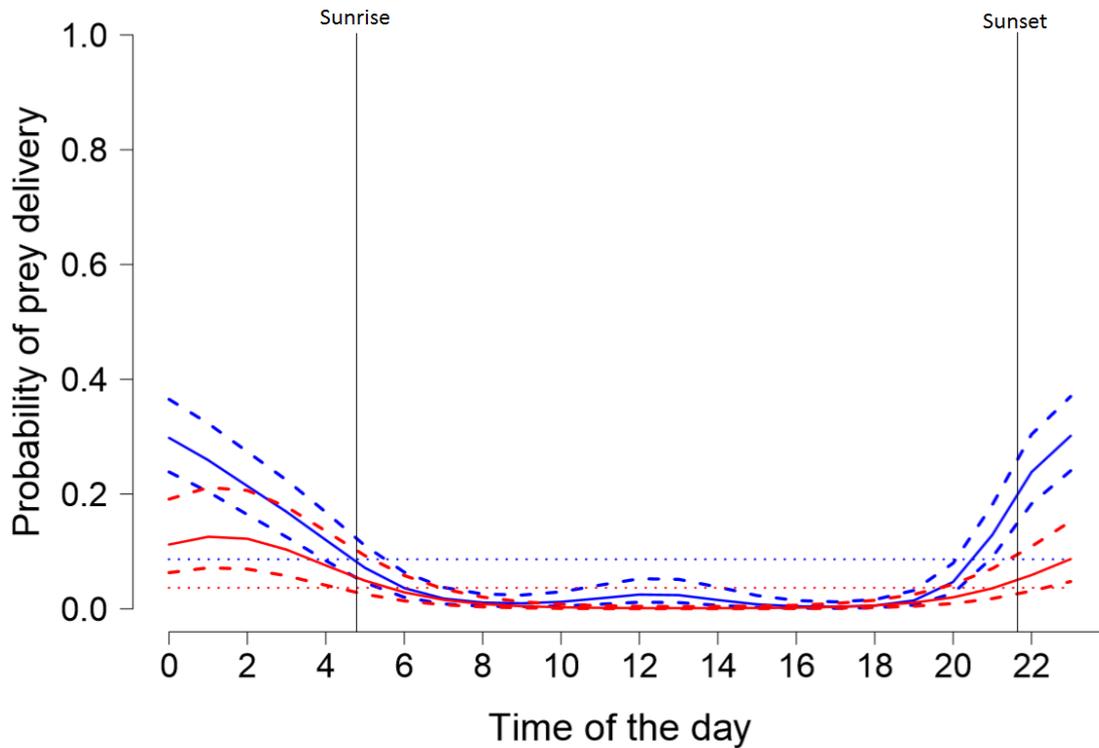


Figure 3: Probability of at least one prey delivery per hour block at tawny owl nests as a function of time of day (h), predicted from models of circadian activity rhythms. Blue denotes mammals and red denotes birds. The dashed lines represent the confidence intervals, while the dotted lines are the midline estimating statistic of rhythm (MESOR). The vertical lines denote average time of sunrise and sunset during the monitoring period.

Among the mammalian prey, the probability of at least one prey delivery peaked at the hour block lasting from 00:00 to 01:00 for field vole, bank vole and wood mouse (Figure 4 (a), (b) and (c), Appendices 5-7), while for shrew the probability peaked one hour block earlier, i.e. from 23:00 to 00:00 (Figure 4 (d), Appendix 8).

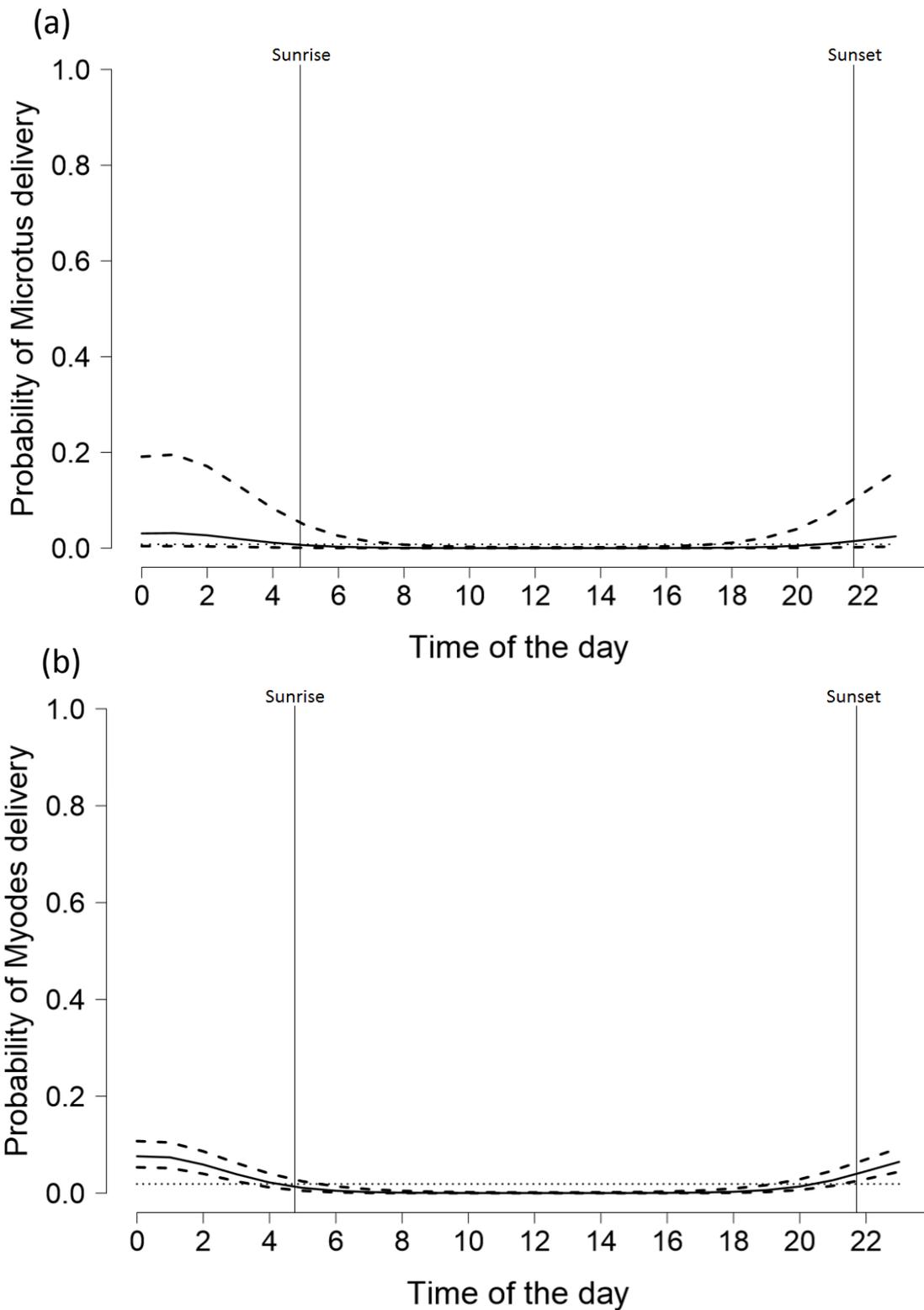
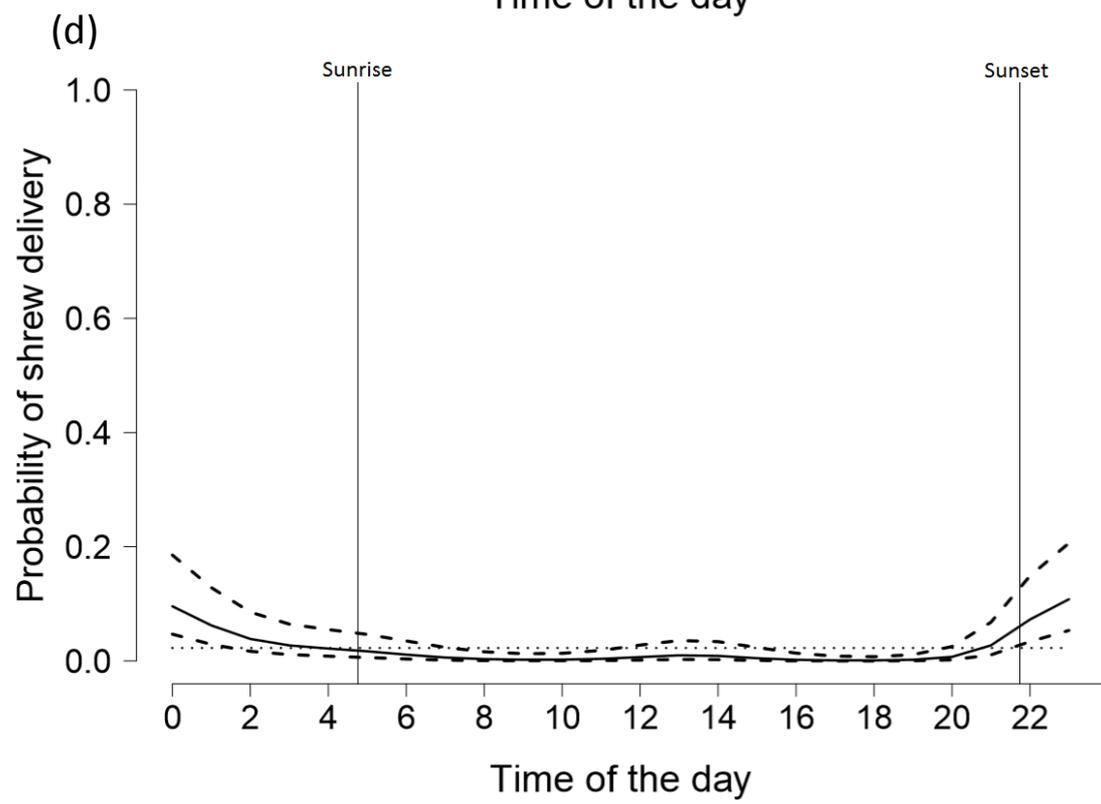
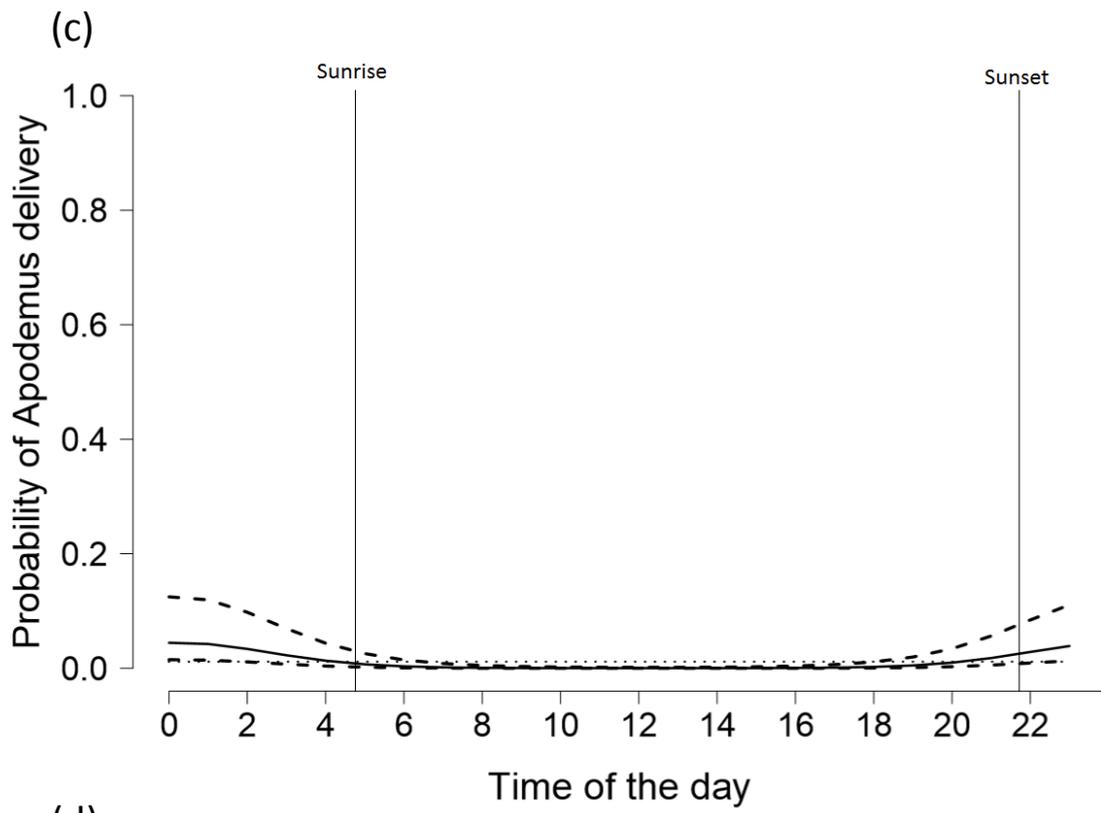


Figure 4: Probability of at least one prey delivery of field vole (*Microtus agrestis*) (a), bank vole (*Myodes glareolus*) (b), wood mouse (*Apodemus sylvaticus*) (c) and shrew (*Soricidae*) (d), per hour block at tawny owl nests as a function of time of day (h), predicted from models of circadian activity rhythms. The two dashed lines represent the confidence interval, while the dotted line is the midline estimating statistic of rhythm (MESOR). The vertical lines denote average time of sunrise and sunset during the monitoring period.



3.3 Prey handling in the nest

The model that best explained the probability that the nestlings ingested a prey item unassisted (AIC = 378.3) included both nestling age and prey body mass as explanatory variables (Figure 5, Table 3). As the nestlings grew older, and as prey body mass decreased, the probability that they ingested a prey item unassisted increased. High nestling age combined with low prey body mass therefore predicted the highest probability of the nestlings ingesting prey unassisted (Figure 5). The switch, when the nestlings ingested the prey unassisted with the same probability as the female assisted with the feeding, occurred when the nestlings were about 9 days old for the smallest prey items, and when the nestlings were about 26 days old for the largest prey items (Figure 5). Based on the model that only included nestling age as an explanatory variable (AIC = 402.5), the switch occurred when the nestlings were about 12 days old (Table 4).

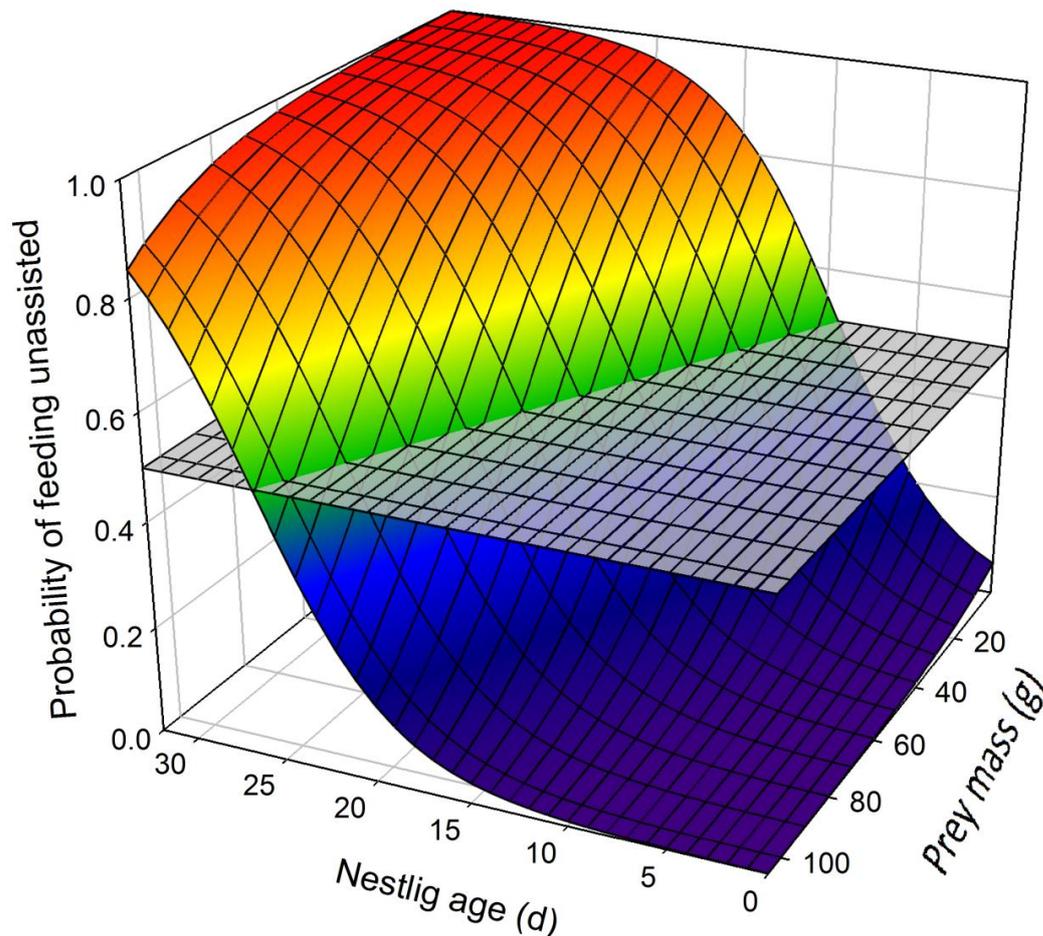


Figure 5: Probability that the tawny owl nestlings ingested a prey item unassisted as a function of nestling age and prey mass. The switch, when the nestlings ingested the prey unassisted with the same probability as the female assisted with the feeding, is shown with a horizontal transparent grid. Nestling age is the age of the youngest 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 = 703, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.708	0.621	-4.36	<0.0001
Nestling age	0.291	0.027	10.73	<0.0001
Prey body mass	-0.046	0.009	-5.22	<0.0001

Table 4: 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). The model is corrected for nest ID (n = 703, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-3.485	0.687	-5.07	<0.0001
Nestling age	0.290	0.026	10.97	<0.0001

3.4 Prey mass consumed per nestling per day

To describe prey mass consumed per nestling per day (24 h) two equally good linear models were found. Both models had prey mass consumed per nestling per day as the response variable, but the explanatory variables were different. One of the models had nestling age as the explanatory variable (Table 5), while the other model had season (i.e. number of days after 25 April, when the monitoring period started at the first nest) as the explanatory variable (Table 6). My data does not give grounds to discriminate between these two models ($\Delta AIC = 1.9$) (Burnham & Anderson 2002).

As the nestlings grew older, the prey mass that each nestling consumed per day increased, from an estimated 33.3 g at an age of 5 days to 53.6 g at an age of 25 days (Figure 6). The same was the case as time elapsed after the monitoring period started, but here the increase was from an estimated 29.2 g after 5 days of monitoring to 51.1 g after 25 days of monitoring (Figure 7).

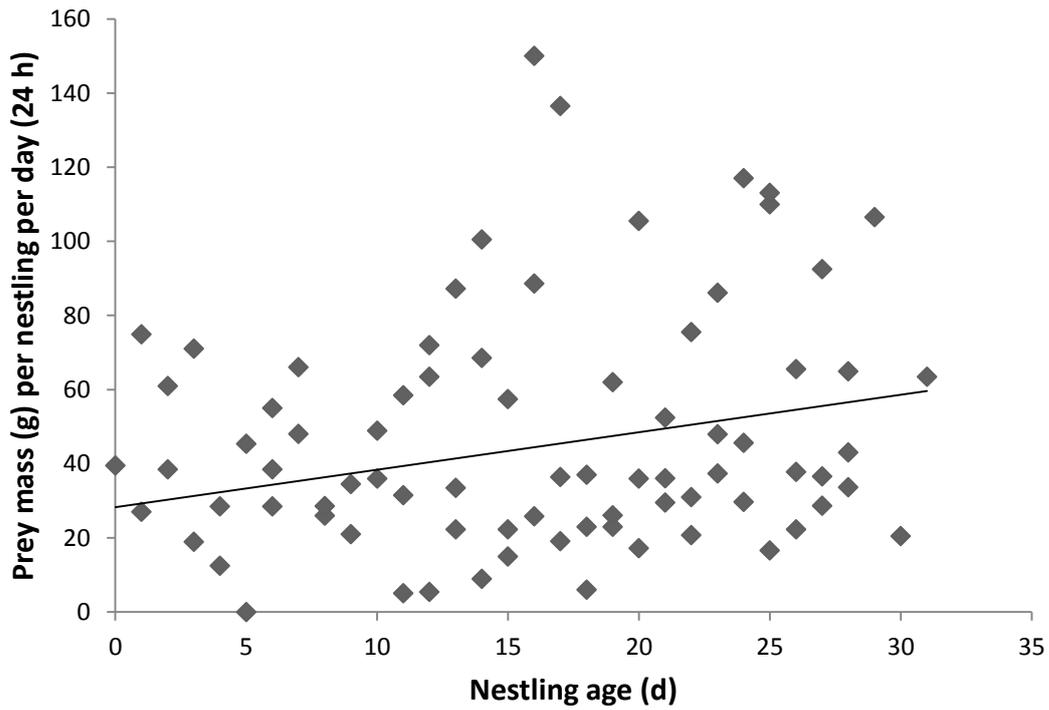


Figure 6: Prey mass consumed per nestling per day (24 h) as a function of nestling age in three nests of the tawny owl.

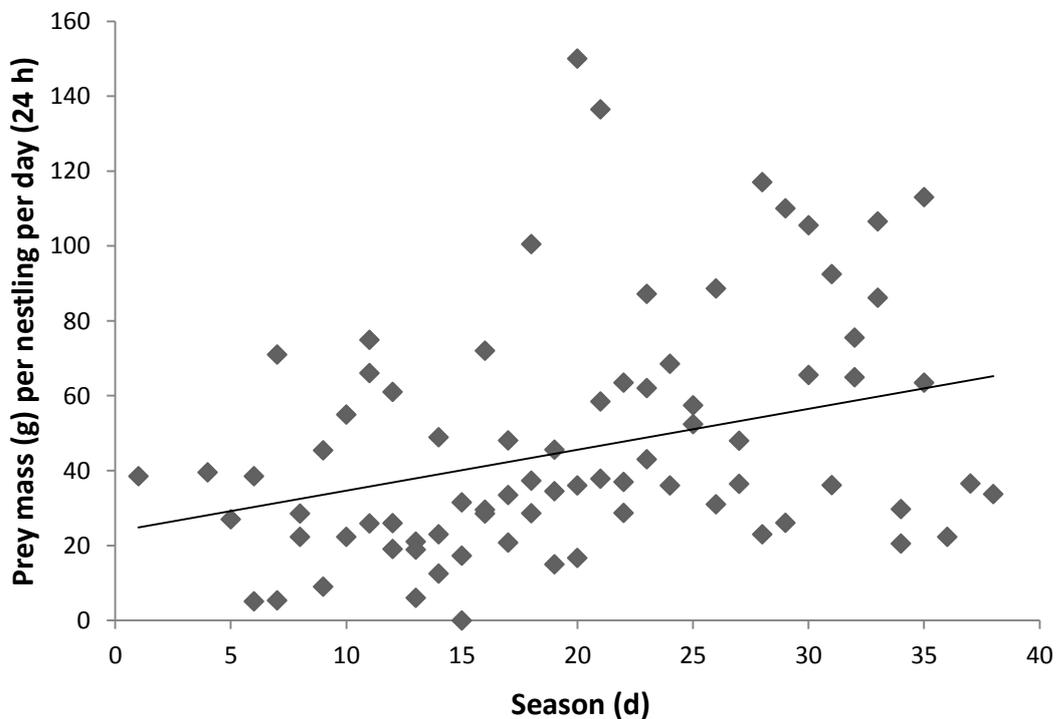


Figure 7: Prey mass consumed per nestling per day (24 h) as a function of season (i.e. number of days after 25 April, when the video monitoring period started) in three nests of the tawny owl.

Table 5: Parameter estimates from the model of prey mass (g) consumed per nestling per day (24 h) as a function of nestling age. The model is corrected for nest ID (n = 79, random effect = 3 nests).

	Estimate	SE	t	p
Intercept	28.282	13.313	2.124	0.037
Nestling age	1.011	0.385	2.623	0.011

Table 6: Parameter estimates from the model of prey mass (g) consumed per nestling per day (24 h) as a function of season. The model is corrected for nest ID (n = 79, random effect = 3 nests).

	Estimate	SE	t	p
Intercept	23.756	11.301	2.102	0.039
Season	1.092	0.379	2.883	0.005

4. Discussion

4.1 Composition of the diet

The tawny owls showed a diverse diet during the breeding season of 2015. By number of the prey items delivered at the three nests at least 36.2 % were invertebrate, at least 32.6 % were mammalian, at least 15 % were avian, at least 2.0 % were amphibian, and at least 1.1 % were reptilian, while 13.1 % were unidentified prey items. By estimated body mass of these prey items at least 56.8 % were mammalian, at least 30.2 % were avian, at least 4.3 % were amphibian, at least 1.2 % were reptilian, and at least 0.9 % were invertebrate, while 6.5 % were unidentified prey items. The tawny owl is often defined as a food generalist (e.g. Galeotti 1990; Galeotti et al. 1991; Goszczyński et al. 1993; Sunde et al. 2001; Zawadzka & Zawadzki 2007), which is also supported by my results. In addition, there were clear differences in the composition of diet between the three nest locations.

The most surprising result regarding choice of prey was the high number of invertebrates delivered at nest location Norderås (60 % of all prey items delivered at this nest). High percentages of invertebrates have also previously been reported in the diet of the tawny owl. Manganaro et al. (2000) reported that invertebrates constituted up to 95 % of prey items by number in lowland oak woods in Central Italy. In my study, location Norderås was probably the nest location with the most similar surroundings to the lowland oak woods in Italy, if one should compare. The nest box at Norderås was situated in a deciduous forest consisting of mostly large ash (*Fraxinus excelsior*) and oak (*Quercus sp.*) trees. This particular area has also previously been described as an important insect biotope (Follorådet (1996) and references therein), which is in line with my findings, since most of the invertebrates that were delivered at the nest at this site were either classified as insects or believed to be insects. It will be interesting to see if the high number of invertebrates in the diet of the tawny owl at this location would be repeated in another breeding season.

Invertebrates are, however, not commonly the main prey of the tawny owl, since rodent are most often reported as being the most numerous species in the diet of the tawny owl, as well as constituting a substantial amount of the total prey mass consumed (e.g. Sunde et al. 2001; Solonen & Karhunen 2002; Žmihorsk & Osojca 2006; Zawadzka & Zawadzki 2007). The exact species of rodents which are most frequently taken by the tawny owl seems, however, to

vary between areas and years (e.g. Balčiauskienė et al. 2005). In my study, shrews were the most frequently captured mammalian prey species, followed by bank vole, field vole and wood mouse. The fact that shrews were the most numerous species is an interesting observation, since snap trapping in the area throughout the years have indicated that shrews are not abundant in the terrain (Geir A. Sonerud, pers. comm.). Shrews, as well as birds and amphibians, have previously been described as alternative prey species for tawny owls in Białowieża National Park in Poland (Jędrzejewski et al. 1996). If shrews were alternative prey for the tawny owls in my study as well, it would indicate that the tawny owl's main prey, small rodents (Cramp 1985), might have had low abundance or were not easily captured by the owl. Prior to the study, the expectation was that the year of my study would be a poorer small rodent year than the previous one, but snap trapping results indicated that the abundance of small rodents was approximately at the same level as the year before (Geir A. Sonerud, pers. comm.), i.e. the year that Stave (2015) video monitored tawny owl nests in the same area that I did. Stave (2015) found wood mouse to be the most common prey of the tawny owl, but also shrews to be numerous. By number, shrews actually constituted a higher percentage in the study of Stave (2015). By looking at the percentages by prey mass for the different prey groups (i.e. mammals, birds, reptiles, amphibians and invertebrates), the results by Stave (2015) did, however, not differ much from my results.

The number of bank voles delivered at the nests in my study was almost equal to the number of wood mice, which also was in accordance with snap trapping results (Geir A. Sonerud, pers. comm.). In addition, the number of field voles delivered at the nests was almost equal to the number of bank voles and wood mice, which is an interesting observation, given that field voles use mostly open habitats (e.g. Corbet & Southern 1977), and the tawny owl has been reported to prefer deciduous forest and avoid open habitats when hunting in my study area (Eldegard 1996). This indicates that the tawny owls have hunted not only in the forests, but also on the borders between forests and more open areas, such as fields and clear-cuts. Shrews, bank voles and wood mice are most common in forests (Geir A. Sonerud, pers. comm.), and the tawny owl's capture of these species was therefore in accordance with the owl's reported preference for forest (Eldegard 1996). The home range of tawny owls in my study area has been reported to be 1-2 km² (Eldegard 1996), and for the nest locations in my study this would indicate home ranges including different vegetation types, both forests and open areas.

In a study from Finland, it has been suggested that the dynamics of the tawny owl is driven by the vole cycle, and that the tawny owl might show a numerical response to prey abundance (Karell et al. 2009). Petty (1999) has, on the other hand, reported that tawny owls in England responded functionally, rather than numerically, to vole abundance. As a food generalist, the tawny owl is, however, able to adapt to various conditions caused by natural fluctuations in prey species density (e.g. Cramp 1985; Zalewski 1994). The diet of tawny owls may therefore reflect the available prey species at the actual site. There might also be other factors involved, for instance individual preferences and hunting skills, as well as different anti-predator strategies in the prey species. Some rodents have for instance been reported to reduce their overall activity, including foraging, as a response to the presence of owls (Eilam et al. 1999), which might make them less available for the owls. The vegetation type and amount of ground cover might also affect the availability of prey (Southern 1954; Southern & Lowe 1968; Balčiauskienė et al. 2005), but detailed data on this was not gathered in my study. This could be interesting to look into in future studies.

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 were active and hunting mostly during the night, from a little before sunset in the evening to around sunrise in the morning. This underlines the fact that the tawny owl is known as a nocturnal species (Cramp 1985). The probability of at least one prey delivery of any kind was highest between 00:00 and 01:00, when the probability was 0.53. Some prey deliveries did occur at daytime as well, which also have been reported to occur during the breeding season of the tawny owl in earlier studies (Cramp 1985). Hunting during the day might be explained by the nestlings' increasing need for food as they grow.

Mammals had an overall higher probability of being delivered within an hour block during the main activity period of the owls compared to the probability of avian prey delivery. Both microtines and shrews show a distinct polyphasic activity pattern (Halle 2000; Merritt & Vessey 2000), i.e. a short-term rhythm in activity that switches between rest and active phases during both day and night. This probably makes these species available for the tawny owl to hunt both day and night, and might explain why some deliveries of shrews, bank voles and field voles occurred at daytime, although most occurred at night. The wood mouse is most

often referred to as a monophasic species (Flowerdew 2000), i.e. the activity pattern shows one long activity phase. Since the wood mouse is nocturnal (Flowerdew 2000), this activity phase occurs at night, which makes the wood mouse an available prey species for the tawny owl to hunt at night.

The probability of at least one avian prey delivery within an hour block showed a similar pattern as for mammalian prey delivery, even though the probability of avian prey delivery within an hour block was overall lower than for mammalian prey delivery. Only 8 out of 107 avian prey deliveries occurred between 06:00 and 21:00, which clearly shows that the availability of avian prey must have been quite high during the night. Why the tawny owl has been able to capture such a high number of avian prey is not easy to pinpoint, but it might have captured roosting birds (Harrison 1960). Bird vocalization during the night might also have contributed to the tawny owl's successful localization and capture of avian prey (Stave 2015), since the tawny owl's hearing is important when it hunts (Cramp 1985).

4.3 Prey handling in the nest

The probability of the tawny owl nestlings feeding unassisted was affected by both the age of the nestlings and the mass of the prey items. When the nestlings grew older, they more frequently ingested prey items unassisted, and the larger the prey items were, the more likely the female was to assist the nestlings with the feeding. Stave (2015) also found a similar pattern. A study of nine raptor species also found that size, as well as type, of prey influenced when the nestlings started to ingest prey unassisted (Sonerud et al. 2014b). The nestlings were more likely to ingest smaller prey items unassisted compared to larger prey items, which the female was more likely to assist with when delivered to the nest (Sonerud et al. 2014b).

As nestlings grow older and larger, their demand for food naturally increases (Barba et al. 2009; Steen 2010). Therefore it might be profitable for foraging parents to deliver larger prey items when the nestlings become older (Slagsvold & Wiebe 2007). At the same time, this might result in higher mortality for the youngest nestlings, whose ability to ingest large prey items is lower than for the older nestlings, if sufficient feeding assistance is not provided (Slagsvold & Wiebe 2007). This is known as the feeding constraint hypothesis (Slagsvold & Wiebe 2007), and it is consistent with my findings in the sense that the need for prey

preparation increases with the size of the prey and decreases with the nestlings' age. In this connection, it was interesting to observe that at one of the nest locations, Kroer, the oldest and largest nestling dragged prey items out of the bill of its younger and much smaller sibling, when the latter had difficulties ingesting the prey items. The size difference between these two siblings was quite pronounced early after hatching, but became less pronounced with time. The reason may have been the seemingly no shortage of food in this nest, making it possible for the youngest nestling to eventually attain a gape size large enough to ingest larger prey items in one piece.

4.4 Prey mass consumed per nestling per day

Linear trends were found between the estimated prey mass consumed per tawny owl nestling per day and nestling age, as well as between the estimated prey mass consumed per nestling per day and season. Based on AIC values the models were equally good, and this did not give grounds for ranking them, since $\Delta AIC < 2.0$ (Burnham & Anderson 2002). According to the model with season as the explanatory variable, the amount of estimated prey mass consumed per nestling per day increased as time elapsed after 25 April, when the monitoring period started at the first nest. The same was the case with the model with nestling age as the explanatory variable. Similar patterns regarding prey mass consumption in tawny owl nestlings have also been reported by Stave (2015).

The increase in prey mass consumed per nestling per day as the nestlings became older might be explained by the nestlings' increasing food demand as they grow. Older and larger nestlings would require more food than younger and smaller nestlings, and the need for energy might be highest when the nestlings' growth rate peak (Barba et al. 2009; Steen et al. 2012). At the same time, the growth rates of nestlings are not constant, and the food demand might vary accordingly (Barba et al. 2009). Whether the linear trend I found between daily food consumption by a nestling and nestling age reflects the growth rate of the nestlings is unknown. To the contrary, one might also suggest that nestlings' growth rate is reflected by the daily amount of food they consume based on what they are provided with by their parents.

According to Cramp (1985), the feeding rate of tawny owls is greatest when the nestlings are 11-25 days old (cf. Steen et al. 2012). If one assumes that a higher feeding rate also meant

more prey mass delivered to the nest and consumed by the nestlings, that would indicate a non-linear trend between a nestling's food consume and nestling age. That is not in accordance with my results, which indicate a linear trend up to fledging, which on average occurred when the youngest nestling was at least 30 days old. At nest location Norderås the fledging of the last nestling was not recorded due to technical difficulties. Age at fledging was, however, in accordance with Cramp (1985), who stated that tawny owl nestlings usually leave the nest when they are 25-30 days old.

According to Barba et al. (2009), feeding rates usually increase with nestling age for some time, but then decreases as the nestlings approaches their maximum body mass. This has been reported for some non-raptorial birds (Grundel 1987; Blondel et al. 1991; Barba et al. 2009). Steen et al. (2012) also showed a non-linear trend between prey mass delivered per nestling per day and nestling age for the Eurasian kestrel. This non-linear trend was shaped like an inverted U (Steen et al. 2012). Based on my data no such trend was found, but one can still not rule out the possibility that a trend like that might have been the case with a longer dataset, since the parents of tawny owls continue to provide food for their nestlings long after fledging (Southern et al. 1954), and my results does not include post-fledging data. To follow the nestlings in the post-fledging period has for instance been done with Tengmalm's owl (*Aegolius funereus*) (Eldegard & Sonerud 2010, 2012), and would be interesting to do in future studies of the tawny owl as well.

The linear model with only season included described equally well the amount of prey mass consumed per nestling per day. This means that the effect of season on the prey mass consumed per nestling per day could not be discriminated from the effect of nestling age based on my data. A linear relationship between the amount of prey mass delivered per nestling and season was also found by Steen et al. (2012) in the Eurasian kestrel, though this model did not fit as well as the one with nestling age. The results by Steen et al. (2012) did, however, deviate from mine, since Steen et al. (2012) reported a decreasing linear trend as time elapsed and my model indicated an increasing linear trend as time elapsed. There is no easy explanation to why the amount of prey mass consumed per nestling per day increased with season, but it might be connected to the availability of prey. As the season progressed, there may have been more available prey. Further studies are, however, needed to separate between these two effects.

5. Conclusion

My results clearly show that the tawny owl is able to utilize a wide range of prey species, including mammals, birds, amphibians and reptiles, as well as earthworms and insects, which was also suspected since the tawny owl is considered to be a food generalist. Snap trapping results of small rodents in the study area indicated that the abundance of small rodents was relatively similar to the previous spring season, when the abundance was considered to be high, and the diet of the tawny owl was studied by Stave (2015). At first sight, the results obtained from the latter year seemed to differ from the results from the previous year. However, due to a high number of small invertebrates registered in the latter year, the estimated prey mass of the different prey groups constituted approximately the same percentages as the previous year. Most prey items, regardless of type, were delivered at the nests at night-time, which is in accordance with the fact that the tawny owl mostly is regarded as a nocturnal species. The delivery of different types of mammalian and avian prey might also be explained by the activity pattern of the prey species. Whether the female assisted the nestlings during feeding rather than the nestlings ingested prey unassisted was affected by both nestling age and prey body mass, with the highest probability of the nestlings ingesting prey unassisted when they were older and the prey body mass was low. Each nestling on average consumed more prey mass per day as it grew older, and as the season progressed. The data did not give grounds to discriminate between these two explanations to the nestling's food consumption, but nestling age seems, however, to be more biological meaningful regarding nestlings' increased food demand and prey mass provided by the parents.

6. References

- Balčiauskienė, L., Juškaitis, R. & Atkočaitis, O. (2005). The diet of the tawny owl (*Strix aluco*) in South-Western Lithuania during the breeding period. *Acta Zoologica Lituanica*, 15 : 13-20.
- Barba, E., Atiénzar, F., Marín, M., Monrós, J. S. & Gil-Delgado, J. A. (2009). Patterns of nestling provisioning by a single-prey loader bird, great tit *Parus major*. *Bird Study*, 56 : 187-197.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.
<http://CRAN.R-project.org/package=lme4>.
- Blondel, J., Dervieux, A., Maistre, M. & Perret, P. (1991). Feeding ecology and life history variation of the blue tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia*, 88 : 9-14.
- Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag. 488 pp.
- Corbet, G. B. & Southern, H. N. (1977). *The handbook of British mammals*. 2nd ed.: Blackwell Scientific Publications. 520 pp.
- Cramp, S. & Simmons, K. E. L. (1980). *The birds of the western palearctic*, vol. II. Oxford: Oxford University Press.
- Cramp, S. (1985). *The birds of the western Palearctic*, vol. IV. Oxford: Oxford University Press.
- Cramp, S. (1988). *The birds of the western Palearctic*, vol. V. Oxford: Oxford University Press.
- Cramp, S. (1992). *The birds of the western Palearctic*, vol. VI. Oxford: Oxford University Press.
- Cramp, S. & Perrins, C. M. (1993). *The birds of the western Palearctic*, vol. VII. Oxford: Oxford University Press.
- Cramp, S. & Perrins, C. M. (1994). *The birds of the western Palearctic*, vol. VIII. Oxford: Oxford University Press.
- Eilam, D., Dayan, T., Ben-Eliyahu, S., Schulman, I., Shefer, G. & Hendrie, C. A. (1999). Differential behavioural and hormonal responses of voles and spiny mice to owl calls. *Animal Behaviour*, 58 : 1085-1093.

- Eldegard, K. (1996). *Home range characteristics and habitat selection of tawny owls (Strix aluco) in southeastern Norway*. Cand. agric. thesis. Ås: Agricultural University of Norway.
- Eldegard, K. & Sonerud, G. A. (2010). Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl. *Behavioral ecology and sociobiology*, 64 : 815-826.
- Eldegard, K. & Sonerud, G. A. (2012). Sex roles during post-fledging care in birds: female Tengmalm's owls contribute little to food provisioning. *Journal of Ornithology*, 153 : 385-398.
- Erkert, H. G. & Kappeler, P. M. (2004). Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae). *Behavioral Ecology and Sociobiology*, 57 : 174-186.
- Flowerdew, J. R. (2000). Wood mice - small carnivores/insectivores with seasonally variable patterns. In Halle, S. & Stenseth, N. C. (eds) *Ecological studies*, vol. 141 *Activity patterns in small mammals : an ecological approach*. Berlin: Springer-Verlag.
- Follorådet. (1996). *Biologisk mangfold i Follo. Rapport 2: Viktige områder for det biologiske mangfoldet i Follo*.
- Galeotti, P. (1990). Territorial behaviour and habitat selection in an urban population of the tawny owl *Strix aluco* L. *Italian Journal of Zoology*, 57 : 59-66.
- Galeotti, P., Morimando, F. & Violani, C. (1991). Feeding ecology of the tawny owls (*Strix aluco*) in urban habitats (northern Italy). *Bollettino Di Zoologia*, 58 : 143-150.
- Goszczynski, J., Jablonski, P., Lesinski, G. & Romanowski, J. (1993). Variation in diet of tawny owl *Strix aluco* L. along an urbanization gradient. *Acta ornithologica*, 27 : 113-123.
- Grundel, R. (1987). Determinants of nestling feeding rates and parental investment in the mountain chickadee. *The Condor*, 89 : 319-328.
- Halle, S. (2000). Voles - small graminivores with polyphasic patterns. In Halle, S. & Stenseth, N. C. (eds) *Ecological studies*, vol. 141 *Activity patterns in small mammals : an ecological approach*. Berlin: Springer-Verlag.
- Halle, S. & Stenseth, N. C. (2000). *Activity patterns in small mammals : an ecological approach*. *Ecological studies*, vol. 141. Berlin: Springer-Verlag. 320 pp.
- Harrison, C. J. O. (1960). The food of some urban tawny owls. *Bird Study*, 7 : 236-240.
- Itämies, J. & Korpimäki, E. (1987). Insect food of the kestrel, *Falco tinnunculus*, during breeding in western Finland. *Aquilo Seriological Zoologica*, 25: 21-31.

- Jaksić, F. M. (1982). Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. *Oecologia*, 52 : 171-175.
- Jędrzejewski, W., Jędrzejewska, B., Szymura, A. & Zub, K. (1996). Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). *Journal of Animal Ecology*, 65 : 105-120.
- Karell, P., Ahola, K., Karstinen, T., Zolei, A. & Brommer, J. E. (2009). Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. *Journal of Animal Ecology*, 78 : 1050-1062.
- Kronfeld-Schor, N. & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, 34: 153-181.
- Manganaro, A., Ranazzi, L. & Salvati, L. (2000). The diet of tawny owls (*Strix aluco*) breeding in different woodlands of Central Italy. *Buteo*, 11 : 115-124.
- Merritt, J. F. & Vessey, S. H. (2000). Shrews - small insectivores with polyphasic patterns. In Halle, S. & Stenseth, N. C. (eds) *Ecological studies*, vol. 141 *Activity patterns in small mammals: an ecological approach*. Berlin: Springer-Verlag.
- Mistlberger, R. E. & Skene, D. J. (2004). Social influences on mammalian circadian rhythms: animal and human studies. *Biological Reviews*, 79 : 533-556.
- Newton, I. (1979). *Population ecology of raptors*. Berkhamsted: T & A D Poyser Ltd. 399 pp.
- Nilsson, I. N. (1978). Hunting in flight by tawny owls *Strix aluco*. *Ibis*, 120 : 528-531.
- Petty, S. J. (1999). Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *Journal of zoology*, 248 : 451-465.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. (2014). nlme: Linear and nonlinear mixed effects models. R package version 3.1-118.
<http://CRAN.R-project.org/package=nlme>.
- Pita, R., Mira, A. & Beja, P. (2011). Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. *Animal Behaviour*, 81 : 1023-1030.
- R Development Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Redpath, S. M. (1995). Impact of habitat fragmentation on activity and hunting behavior in the tawny owl, *Strix aluco*. *Behavioral Ecology*, 6 : 410-413.
- SAS Institute Inc. (2015). JMP Pro version 12.1.0. SAS Institute Inc., Cary, NC.

- Selås, V. (2001). Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Canadian Journal of Zoology*, 79 : 2086-2093.
- Slagsvold, T. & Wiebe, K. L. (2007). Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. *Animal Behaviour*, 73 : 691-700.
- Slagsvold, T., Sonerud, G. A., Grønlien, H. E. & Stige, L. C. (2010). Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology*, 41 : 488-497.
- Solonen, T. & Karhunen, J. (2002). Effects of variable feeding conditions on the tawny owl *Strix aluco* near the northern limit of its range. *Ornis Fennica*, 79 : 121-131.
- Sonerud, G. A. (1994). Kattugle *Strix aluco*. In Gjershaug, J. O., Thingstad, P. G., Eldøy, S. & Byrkjeland, S. (eds) *Norsk fugleatlas*. Klæbu: Norsk Ornitologisk Forening.
- Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2013). Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. *Oecologia*, 172 : 93-107.
- Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014a). Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. *Animal Behaviour*, 96 : 31-38.
- Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G. H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., et al. (2014b). Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology*, 25 : 762-772.
- Southern, H. N. (1954). Tawny owls and their prey. *Ibis*, 96 : 384-410.
- Southern, H. N., Vaughan, R. & Muir, R. C. (1954). The behaviour of young tawny owls after fledging. *Bird Study*, 1 : 101-110.
- Southern, H. N., & Lowe, V. P. W. (1968). The pattern of distribution of prey and predation in tawny owl territories. *Journal of Animal Ecology*, 37 : 75-97.
- Stave, M. (2015). *Prey deliveries at nests of the tawny owl (Strix aluco): diet and diel pattern*. MSc thesis. Ås: Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management.
- Steen, R. (2009). A portable digital video surveillance system to monitor prey deliveries at raptor nests. *Journal of Raptor Research*, 43 : 69-74.

- Steen, R. (2010). *Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (Falco tinnunculus)*. Ph.D. thesis. Ås: Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management.
- Steen, R., Sonerud, G. A. & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (*Falco tinnunculus*). *Journal of Ornithology*, 153 : 1087-1099.
- Sunde, P., Overskaug, K., Bolstad, J. P. & Øien, I. J. (2001). Living at the limit: ecology and behaviour of tawny owls *Strix aluco* in a northern edge population in central Norway. *Ardea*, 89 : 495-508.
- Systat Software Inc. (2008). SigmaPlot version 11.0. Systat Software Inc., San Jose, CA.
- Zalewski, A. (1994). Diet of urban and suburban tawny owls. *Journal of Raptor Research*, 28 : 246-252.
- Zawadzka, D. & Zawadzki, J. (2007). Feeding ecology of tawny owl (*Strix aluco*) in Wigry national park (North east Poland). *Acta Zoologica Lituanica*, 17 : 234-241.
- Żmihorsk, M. & Osojca, G. (2006). Diet of the tawny owl (*Strix aluco*) in the Romincka forest (north east Poland). *Acta Zoologica Lituanica*, 16 : 54-60.

Appendix



Appendix 1: The male tawny owl at nest box location Kroer delivers a prey to the nestlings.

Appendix 2: Parameter estimates from the model of the probability of at least one prey delivery of any kind per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-2.354	0.228	-10.33	< 0.0001
I(cos(2 * pi * Hour/24))	1.877	0.128	14.70	< 0.0001
I(sin(2 * pi * Hour/24))	0.562	0.166	3.39	0.0007
I(cos(2 * 2 * pi * Hour/24))	0.965	0.144	6.72	< 0.0001
I(sin(2 * 2 * pi * Hour/24))	0.0493	0.149	0.33	0.74
I(cos(3 * 2 * pi * Hour/24))	-0.365	0.124	-2.95	0.0032
I(sin(3 * 2 * pi * Hour/24))	-0.329	0.119	-2.77	0.0056

Appendix 3: Parameter estimates from the model of the probability of at least one mammalian prey delivery per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-3.236	0.174	-18.55	< 0.0001
I(cos(2 * pi * Hour/24))	1.751	0.175	9.98	< 0.0001
I(sin(2 * pi * Hour/24))	0.561	0.240	2.34	0.020
I(cos(2 * 2 * pi * Hour/24))	0.977	0.205	4.76	< 0.0001
I(sin(2 * 2 * pi * Hour/24))	0.0268	0.209	0.13	0.90
I(cos(3 * 2 * pi * Hour/24))	-0.348	0.167	-2.081	0.037
I(sin(3 * 2 * pi * Hour/24))	-0.373	0.160	-2.34	0.019

Appendix 4: Parameter estimates from the model of the probability of at least one avian prey delivery per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-4.316	0.377	-11.46	< 0.0001
I(cos(2 * pi * Hour/24))	2.247	0.292	7.71	< 0.0001
I(sin(2 * pi * Hour/24))	0.799	0.205	3.89	0.0001

Appendix 5: Parameter estimates from the model of the probability of at least one prey delivery of field vole per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-6.301	1.106	-5.70	< 0.0001
I(cos(2 * pi * Hour/24))	2.847	0.534	5.33	< 0.0001
I(sin(2 * pi * Hour/24))	0.485	0.304	1.60	0.11

Appendix 6: Parameter estimates from the model of the probability of at least one prey delivery of bank vole per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-5.576	0.491	-11.36	< 0.0001
I(cos(2 * pi * Hour/24))	3.0801	0.575	5.35	< 0.0001
I(sin(2 * pi * Hour/24))	0.280	0.301	0.93	0.35

Appendix 7: Parameter estimates from the model of the probability of at least one prey delivery of wood mouse per hour block (n = 2263, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-5.859	0.706	-8.31	< 0.0001
I(cos(2 * pi * Hour/24))	2.793	0.549	5.084	< 0.0001
I(sin(2 * pi * Hour/24))	0.174	0.308	0.57	0.57

Appendix 8: Parameter estimates from the model of the probability of at least one prey delivery of shrew per hour block (n = 2264, random effect = 3 nests).

	Estimate	SE	z	p
Intercept	-4.643	0.425	-10.91	< 0.0001
I(cos(2 * pi * Hour/24))	1.442	0.286	5.043	< 0.0001
I(sin(2 * pi * Hour/24))	0.453	0.401	1.13	0.26
I(cos(2 * 2 * pi * Hour/24))	1.026	0.354	2.90	0.0037
I(sin(2 * 2 * pi * Hour/24))	0.192	0.329	0.58	0.60
I(cos(3 * 2 * pi * Hour/24))	-0.0699	0.273	-0.26	0.80
I(sin(3 * 2 * pi * Hour/24))	-0.727	0.285	-2.55	0.011



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