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Prey deliveries at nests of the tawny owl (*Strix aluco*): diet and diel pattern

Leveringer av byttedyr på reir av
kattugle (*Strix aluco*): diett og
døgnmønster

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ABSTRACT

I used continuous video monitoring to record prey items delivered at four tawny owl (*Strix aluco*) nests in Akershus county in southeast Norway during May 2014. A total of 1635.5 hours of video recordings were gathered, and 531 prey items were registered, giving a total of 14456 g of delivered prey mass. Mammals were the largest prey group in total with 66% of the prey items and 58% of delivered prey mass. The most commonly delivered prey species was the wood mouse (*Apodemus sylvaticus*), contributing with 27% of delivered prey items and 25% of total prey mass. Birds were also a large part of the tawny owl diet, with 18% of prey items by number and 34% of the prey mass. Other prey delivered were reptiles (0.5% by number and 0.3% by mass), amphibians (5% by number and 4% by mass) and invertebrates (1.7% by number and < 0.1% by mass). The probability of one or more prey deliveries per hour block peaked between sunset and sunrise for all prey types. The probability of delivery of a mammalian prey was highest before midnight, whereas birds had the highest probability of being delivered after midnight. For mammalian prey species, a diel pattern of delivery matching that of the prey species was found. The same was true for the avian prey, where the probability of a prey being a thrush (Turdidae) which is more adapted for nocturnal activity, rather than another passerines (Passeriformes) less adapted for nocturnal activity, differed between adult and young of the year, and between prey delivery in the evening and in the morning. The probability of a prey delivered being a shrew (Soricidae) rather than another prey type decreased with nestling age, whereas the probability of a prey being a bird rather than another prey type increased with nestling age. The probability of a prey item being a bird rather than another prey type increased with the date as well. The probability of a prey being decapitated was low, but increased with the size of the prey. The nestlings' need for feeding assistance from the female increased with prey mass and decreased with the age of the nestlings. The prey mass consumed per day per tawny owl nestling increased with nestling age, and in a non-linear model peaked at an age of 16-17 days.

SAMMENDRAG

Jeg brukte sammenhengende videoobservasjon til å registrere byttedyrleveringer på fire reir med kattugle (*Strix aluco*) i Akershus fylke, Sørøst-Norge i mai 2014. Det ble totalt samlet inn 1635,5 timer med videopptak, og 531 bytter ble registrert, som ga en total på 14456 g levert byttedyrmasse. Pattedyr var den største gruppa av byttedyr, med 66% av antall leverte individer og 58% av den totale byttedyrmassen. Den vanligste byttedyrarten var skogmus (*Apodemus sylvaticus*) som bidro med 27% av de leverte byttedyrene, og utgjorde 25% av den totale byttedyrmassen. Fugler utgjorde også en stor del av kattuglas diett, med 18% av byttedyrene i antall og 34% av byttedyrmassen. Andre byttedyr som ble levert var reptiler (0,5% i antall og 0,3% i masse), amfibier (5% i antall og 4% i masse) og invertebrater (1,7% i antall og < 0,1% i masse). Sannsynligheten for en eller flere byttedyrleveringer per timesblokk var høyest mellom solnedgang og soloppgang for alle typer byttedyr. Sannsynligheten for levering av et pattedyr var høyest før midnatt, mens fugler hadde høyest sannsynlighet for levering etter midnatt. For pattedyrene fant jeg et 24-timers leveringsmønster som overensstemte med byttedyrenes aktivitetsmønster. Det samme gjaldt også for fuglene, hvor sannsynligheten for at et byttedyr var en trost (*Turdidae*) som er mer tilpasset til å være nattaktiv, enn en annen spurvefugl (*Passeriformes*) som er mindre tilpasset til å være nattaktiv, varierte mellom voksne og årsgamle unger, og mellom byttedyrleveringer på kvelden og på morgenen. Sannsynligheten for at et levert byttedyr var en spissmus (*Soricidae*) istedenfor en annen byttedyrtype avtok med reirungenes alder, mens sannsynligheten for at et byttedyr var en fugl istedenfor en annen byttedyrtype økte. Sannsynligheten for at et bytte var en fugl fremfor en annen byttedyrtype økte også med datoen. Sannsynligheten for at et bytte var dekapitert var lav, men økte med byttedyrets størrelse. Ungenes behov for fôringshjelp fra hunnen økte med byttedyrets størrelse og avtok med ungenes alder. Byttedyrmassen som ble konsumert per dag av kattugleungene økte med ungenes alder, og hadde en topp ved en alder på 16-17 dager i den ikke-lineære modellen.

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1. INTRODUCTION

The nestlings of raptors are solely dependent on their parents for survival for the first weeks of their life (Sonerud, Steen, Løw et al. 2014). Raptors have a long period of pre- and post-fledging parental care compared to most other birds (Newton 1979). The newly hatched nestlings need warmth and protection from the adult female to survive, and the parents are also the sole providers of food from hatching until fledging (Newton 1979). When the offspring leave the nest, the parents keep providing them with food until they are capable of flying and hunting themselves (Newton 1979). For some species, the post-fledging parental care can last for several months (Eldegard & Sonerud 2010), underlining the importance of committed parents for the survival of the offspring.

Social monogamy is the most common mating pattern in birds, and raptors are no exception (Ketterson & Nolan 1994; Gross 2005). A female-biased size dimorphism, i.e. the female is larger than the male, is found in most of the raptors (Korpimäki 1986b), which correlates with the sex roles during breeding (Sonerud, Steen, Løw et al. 2014). Although the male and female share the burden of raising the offspring, their parental roles are asymmetrical (Sonerud et al. 2013). In the brooding period, the male typically takes on a larger hunting responsibility, while the female tends to the nestlings (Eldegard & Sonerud 2010; 2012). The female start assisting the male in food gathering when the nestlings are less dependent on her for brooding and prey preparation (Sonerud, Steen, Løw et al. 2014). The timing of the start of female hunting seems to correlate with prey types available, as the need for prey preparation varies between prey types and prey sizes (Sonerud, Steen, Selås et al. 2014).

Preparation of prey prior to self-feeding or feeding it to nestlings is not common among birds (Slagsvold et al. 2010). As most raptors take prey items which they are not capable of swallowing or feeding whole, the need to prepare the prey before delivery arises (Slagsvold & Sonerud 2007). This is especially important when the prey is larger, because it is more energy efficient to transport and deliver a prey where the indigestible parts are removed in prior (Sodhi 1992). Slagsvold et al. (2010) showed that the raptors avoided consuming less digestible parts of larger prey.

The tawny owl (*Strix aluco*) is considered a food generalist, with a diet including small mammals, birds, amphibians, insects and earthworms (Cramp 1985). It is primarily known as a forest species, but can be found in a wide range of habitats, including farmland, mountain ranges and urban areas (Obuch 2011). The size of the tawny owl territory varies with habitat type and quality (Hirons

1985), and it has shown to have a home range of 1-2 km² in south-eastern Norway in the breeding season (Eldegard 1996). The tawny owl will commonly use tree cavities for nesting, but will also use other types of suitable cavities, including nest boxes when available (Cramp 1985). When hunting, both beak and claws are used (Cramp 1985), and the species is considered to be mainly nocturnal (Martin 1990). The tawny owl can hunt in flight, but mostly uses the “sit-and-wait” approach (Redpath 1995). Obuch (2011) found 89 different prey species based on dissection of pellets from the tawny owl, showing the diversity of its diet. The populations level and annual breeding success of the tawny owl in all areas tend to follow the cyclic rodent populations (Karell et al. 2009), underlining that rodents are an important food source for the species when available. When the small mammal population is low, the breeding success of the tawny owl has been observed to be noticeably reduced (Jędrzejewski et al. 1996).

Most of today's knowledge of the choice and handling of prey by the tawny owl is derived from the dissection of regurgitated owl pellets (e.g. Galeotti et al. 1991; Balčiauskienė et al. 2006), from dissection of prey remains (e.g. Balčiauskienė 2005) and from direct field observations (e.g. Solonen 2009). Sound recordings have also been used to determine feeding frequency and begging calls in the nest (e.g. Sasvári & Hegyi 2010). Although these methods provide valuable information, they may give incomplete answers. Errington (1930; 1932) warned fellow scientists of the drawbacks of using dissection of owl pellets or prey remains as the only source of diet choice when studying raptor diets as early as in the 1930s, and with good cause. Redpath et al. (2001) showed that dietary conclusions based solely on dissection of prey remains or regurgitated pellets gave skewed estimates regarding the amount of prey of different sizes and taxa. Thus, another, more accurate method for the estimation of raptor diet is needed. Using video monitoring to study prey deliveries in raptors has become more common over the latter years (e.g. Steen 2009; Sonerud, Steen, Selås et al. 2014). Thus, I used video cameras to record prey deliveries at tawny owl nests, and to analyze their diel activity pattern, diet and preparation of prey.

The objective of my study was to gain accurate estimates of the diel pattern of prey deliveries and the choice of prey in the tawny owl, through video monitoring of nest boxes from hatching until fledging. The obtained information was used to i) identify prey items delivered to the nestlings; ii) analyze the diel activity of the tawny owl parents; iii) investigate how nestling age affected the choice of prey; iv) investigate to which extent each prey type was prepared prior feeding and the extent of feeding assistance needed by the parents, and; v) estimate the prey mass delivered to the nestlings.

2. METHODS

2.1 Species and study area

The study area was located in Akershus county in south-eastern Norway, within 12 km from the town of Ås (59°40" N; 10°47" E). The four locations (hereafter referred to as K1, K2, K3 and K4) were in two different areas, K1 located with K2, and K3 with K4. Within each of the two areas, the two nest boxes had 0.9 and 1.7 km between them, and the two areas were located approximately 11 km from each other (Appendix 1). Prior to the field work, all four locations were confirmed to have hatched tawny owl nestlings in the nest boxes. The nest boxes were situated in large trees with surrounding forest patches. Forest type in the surrounding areas mainly consisted of Norway spruce, but at one of the locations, a larger portion of the forest was mixed. Agricultural fields were present nearby in all areas, as well as spread residential and agricultural buildings. The ocean was in the immediate vicinity of nest box K1.

2.2 Video observation

A total of 1635.5 hours of video from the tawny owl nests boxes was recorded between 4th and 29th of May in 2014. The video monitoring at a location was initiated when the youngest nestling was approximately 7 days old. The field work was terminated when all nestlings had fledged. A small bullet CCD camera with IR light was mounted in each of the four nest boxes prior to the observation period. The camera was attached to the wall under the lid of the nest box and was facing the entrance hole, similar to Steen (2009). The camera was connected with a video cable to a hidden, ground mounted digital video recorder (DVR). At location K1, the recordings were stored using a Sony RDR-HX910 DVR powered from the local grid. At location K2, a Sanyo DSR-300 P DVR was used for the first half of the period, and a Real Time H.264 DVR was used for the second half. Both were powered from the local grid. At locations K3 and K4, Cybereye-Mini DVRs (DV-100) stored the videos on 32 GB SD-cards (separated into clips ranging from 5-120 s). The latter recorders were powered by 12V 80AH batteries. The batteries were changed every 7 to 10 days during the observation period, while the SD-cards were changed every 2 to 4 days, ensuring that they always had at least 30% storage space left. All video stored on SD-cards were transferred to an external hard drive for storage, using a PC and a SD-card reader. The video monitoring systems were recording 10-30 frames per s and were recording continuously for the duration of the

observation period.

2.3 Video analysis

The video recordings were reviewed between August 2014 and February 2015. The videos from locations K1 and K2 were reviewed using the DVRs connected to a TV-screen. The videos from locations K3 and K4 were reviewed connecting the external hard drive to a PC, and using the video software XnView, version 2.25. Tawny owl parental activity was recorded in an Apache OpenOffice Calc document, which was later transformed to a Microsoft Excel document. All parental activity inside the nest boxes was noted, including arrivals with prey. The date and time of the parents' arrival at the nest, departure from the nest, and feeding moment was noted, as well as the duration of the female's stay inside the nest box.

The prey items were later identified to species if possible by me, Geir A. Sonerud and Vidar Selås. Some of the prey items delivered were not identifiable due to the angle of the camera, the condition of the prey, the delivery speed or the high activity level of the nestlings. Some of the nest boxes rendered species identification difficult when the nestlings were older, especially in nest boxes where the entrance hole was placed close to the bottom of the nest box (Appendix 2).

Avian prey were identified from the amount, type and coloration of the feathers, the length and size of the beak, body size and overall appearance. Stuffed specimens of tawny owl and small birds were used for a rough, visual size comparison. Mammalian prey were identified from their body size, shape and size of ears, length and shape of the nose, tail length, fur type, size of eyes and overall appearance. Reptiles, frogs, insects and worms were identified by size and appearance.

There was some uncertainty around the identification process for frogs (*Rana* sp.) and shrews (*Soricidae* sp.). Most captured shrews were believed to be common shrew (*Sorex araneus*), except for one registered individual of Eurasian water shrew (*Neomys fodiens*). However, we could not rule out the possibility that some individuals of Eurasian pygmy shrew (*Sorex minutus*) may have been overlooked. The same is true for the frogs, whereas most individuals were believed to be common frog (*Rana temporaria*), but some may have been moor frog (*Rana arvalis*). This was due to the video circumstances.

2.4 Prey body mass estimation

Prior to the statistical analysis, all prey items were assigned an estimated body mass. Annual snap trapping of small mammals has been conducted in the study area since 1993, so the body mass and population levels of the small mammals in spring are well-researched subjects (Geir A. Sonerud pers. comm.). The average body mass of the bank vole (*Myodes glareolus*), field vole (*Microtus agrestis*), wood mouse (*Apodemus sylvaticus*) and the shrews used in this study are derived from these snap trapping results. The body mass assigned to the avian prey species were obtained from an estimated average of Fennoscandian research done by Selås (2001) and Cramp (1985; 1988; 1992), as adult avian individuals tend to have approximate constant body mass (Sonerud et al. 2013). The fledglings were assigned the same body mass as the adults, whereas the mass of the nestlings were reduced by 20% of the average adult mass (Steen 2010).

The slow worms (*Anguis fragilis*) registered were given an average predicted mass of 15 g, by the same method as for avian prey. Because of a large, visual size difference in the delivered individuals of frogs, the frog items were assigned to size groups of either “small” (10 g), “medium” (20 g) or “large” (30 g), based on results from snap trapping in Trysil, Norway in 2008 (Geir A. Sonerud pers. comm.). For insects, the average body mass was obtained from a study done by Itämies and Korpimäki (1987) in Finland. The average body mass of earthworms (Lumbricidae sp.) was estimated from weighing a selection of individuals near the observation area. Unidentified prey items were assigned a mass estimate based on all registered prey items.

2.5 Statistical analysis

The statistical software program R (version 3.1.0), and the ‘nlme’ and ‘lme4’ packages were used to analyze the results gathered from the video analysis. Mixed-effect regression models (logistic and linear regression) were used to analyze the probability of prey delivery and prey handling of the tawny owl (reptiles, amphibians and invertebrates were excluded). When analyzing the probability of prey delivery as a function of time of the day, the periodic components of the time series were set as sine and cosine functions in order to analyze patterns in the circadian rhythm of the tawny owl activity, as shown by Pita et al. (2011). The sample unit was the hours of the day divided into hour blocks, from 0 to 24 for each 24 h period, and was expressed as x in the formula. The probability for a prey to be delivered at a certain hour block was set as the response variable. One or more prey

deliveries within each hour block was scored as “yes”, and no deliveries was scored as “no”, making this a conservative test. The scores were made for all prey in total, and for each prey group. “Breeding pair ID” (expressed as ϵ) was added as a random variable to take the inter-pair variation into account, and to control for duplicate measurements for the owl pair (Pinheiro & Bates 2000). AICc values (Akaike 1978) were used to compare the different model fits (M_1 - M_5) with a random model (M_0), and sorted according to how well the different models fitted according to the AICc values (Burnham & Anderson 2002).

These formulas for the activity models were used:

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

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

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

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

$$M_5: \text{logit}(f(x)) = a_0 + \left(a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24} \right) + \left(a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24} \right) + \left(a_3 \cos \frac{3*2\pi x}{24} + b_3 \sin \frac{3*2\pi x}{24} \right) + \left(a_4 \cos \frac{4*2\pi x}{24} + b_4 \sin \frac{4*2\pi x}{24} \right) + \epsilon$$

Further, the probability of an avian prey to be a thrush rather than another passerine bird was tested as the response variable, where the explanatory variable was the time of day (before or after midnight). All prey groups were tested for the probability that the given prey type was delivered, rather than another prey type, with the nestling age as the explanatory variable. With the response variable set as the probability of delivery of an avian prey, season was used as the explanatory variable. In addition, the probability of a prey to be decapitated upon delivery at a tawny owl nest with prey mass (g) as the explanatory variable was also tested, and a switch test was done for the probability that the nestlings would ingest a prey item unassisted, with prey mass (g) and nestling age (d) as the explanatory variables. Finally, the prey mass consumed per nestling per day was tested, with prey mass (g) as the response variable and nestling age (d) as the explanatory variable. Nest ID was included as a random effect in all tests.

3. RESULTS

3.1 Choice of prey

A large variation of prey was delivered at the tawny owl nests during the observation period. In total, 531 prey items were recorded. Mammals constituted the most numerous prey group with 351 prey items (66%), followed by birds (18.3%), amphibians (5.1%), invertebrates (5.1%) and reptiles (0.5%). The wood mouse was by far the most common prey, making up 42.3% of mammalian prey items, and 27.3% of total prey. Shrews were also numerous, with 16.2% of all prey. Of the prey items delivered, 5.3% could not be identified (Table 1, Appendix 2). The mammalian prey also constituted the most important prey group in terms of estimated prey mass, with 57.8% of the total delivered mass. Birds was the next largest group in terms of mass delivered with 33.5%, followed by amphibians (3.7%), reptiles (0.3%) and invertebrates (< 0.01%). Unidentified prey made up 4.7% of the total anticipated prey mass (Table 1, Appendix 2).

Table 1: Prey deliveries to the tawny owl nests distributed on prey types, with number of items and percentage by number, average body mass, total body mass and percentage by mass.

Prey type	Number of prey	% by number	Average body mass (g)	Total mass (g)	% by mass
Shrew (Soricidae sp.)	86	16.2	10*	860	6.0
Mountain hare (<i>Lepus timidus</i>)	2	0.3	207.5	415	2.9
Bank vole (<i>Myodes glareolus</i>)	46	8.6	22*	1012	7.0
European water vole (<i>Arvicola amphibius</i>)	4	0.7	100	400	2.8
Field vole (<i>Microtus agrestis</i>)	49	9.2	32*	1568	10.9
Unidentified Cricetidae	5	0.9	27	135	0.9
Wood mouse (<i>Apodemus sylvaticus</i>)	145	27.3	25*	3625	25.0
Unidentified small rodent	5	0.9	26	130	0.9
Unidentified small mammal	9	1.7	22	198	1.4
Bird	69	13.0	64**	4416	30.5
Unidentified small bird	28	5.3	15	420	3.0
Slow worm (<i>Anguis fragilis</i>)	3	0.5	15	45	0.3
Frog (<i>Rana</i> sp.)	27	5.1	20	540	3.7
Earthworm (Lumbricidae sp.)	18	3.3	0.8	14.4	0.1
Insect	9	1.7	0.2	1.8	< 0.1
Unidentified prey	26	5.3	26	676	4.7
Total	531	100.0		14456.2	100.0

*Estimated from snap trapping in Ås, spring 1993-2015.

**Estimated average of all identified birds.

3.1.1 Prey delivery according to time of day

The probability of at least one prey delivery per hour block showed a circadian activity rhythm (Figure 1). Deliveries during daytime had a low probability overall. During the study period, solar midnight occurred around 01:15 hours, with sunrise around 05:00 hours in my study area, and sunset around 21:30 hours. There was a peak in the probability of prey deliveries of any kind between 22:00 and 23:00 hours with a probability of 0.7. Another peak occurred after solar midnight, between 02:00 and 03:00 hours with a probability of 0.65, showing that the probability for a delivery was slightly higher before and after the darkest hour (Figure 1).

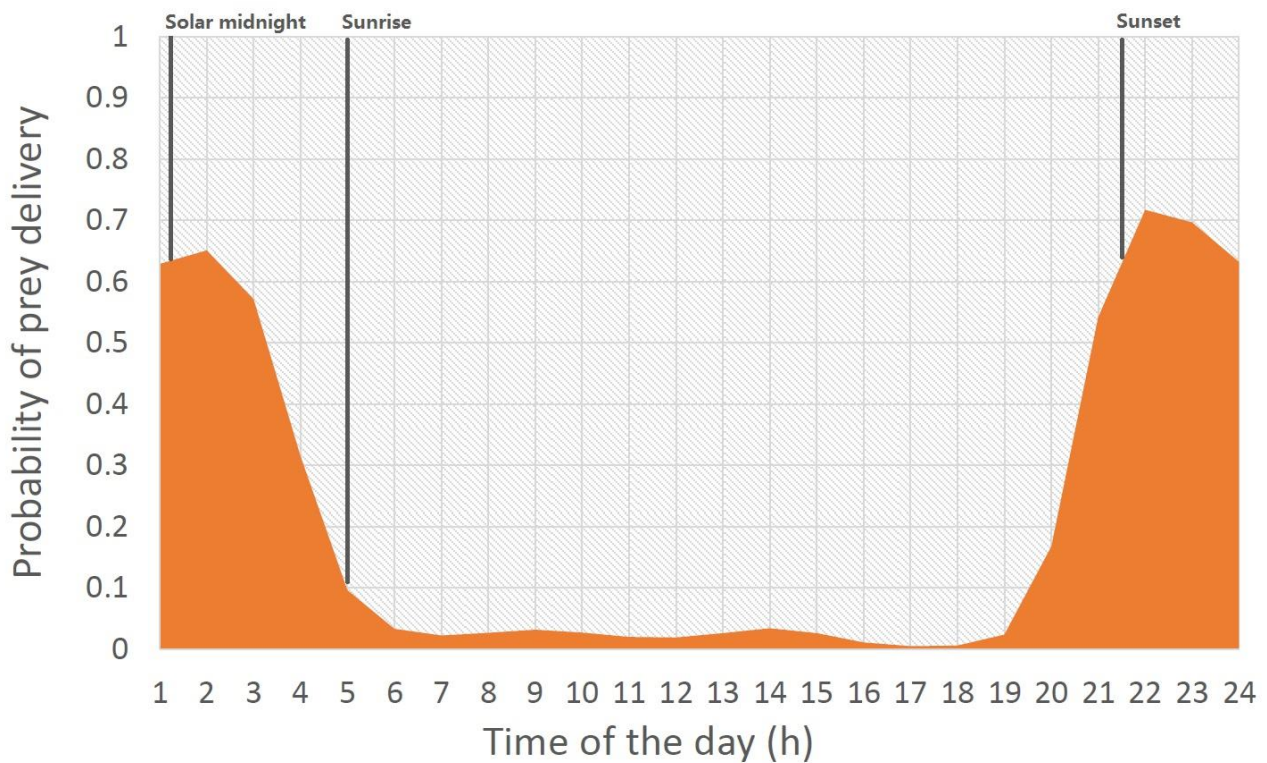


Figure 1: Probability of at least one prey delivery per hour block to a tawny owl (*Strix aluco*) nest as a function of time of day, predicted from models of circadian activity rhythms. The value for hour (n) concerns the time interval from hour n to hour $n+1$.

The probability per hour block for a given prey to be a mammal rather than a bird was higher at all times of the day, showing that a larger part of the tawny owl diet was mammalian rather than avian. The probability for delivery of at least one mammalian prey peaked between 22:00 h and 24:00 h with 0.61 per hour block, whereas the probability for avian delivery peaked between 03:00 h and

04:00 h with 0.15 (Figure 2). There was almost no probability of avian prey being delivered during daytime, and minor probability of mammalian prey during day (Figure 2).

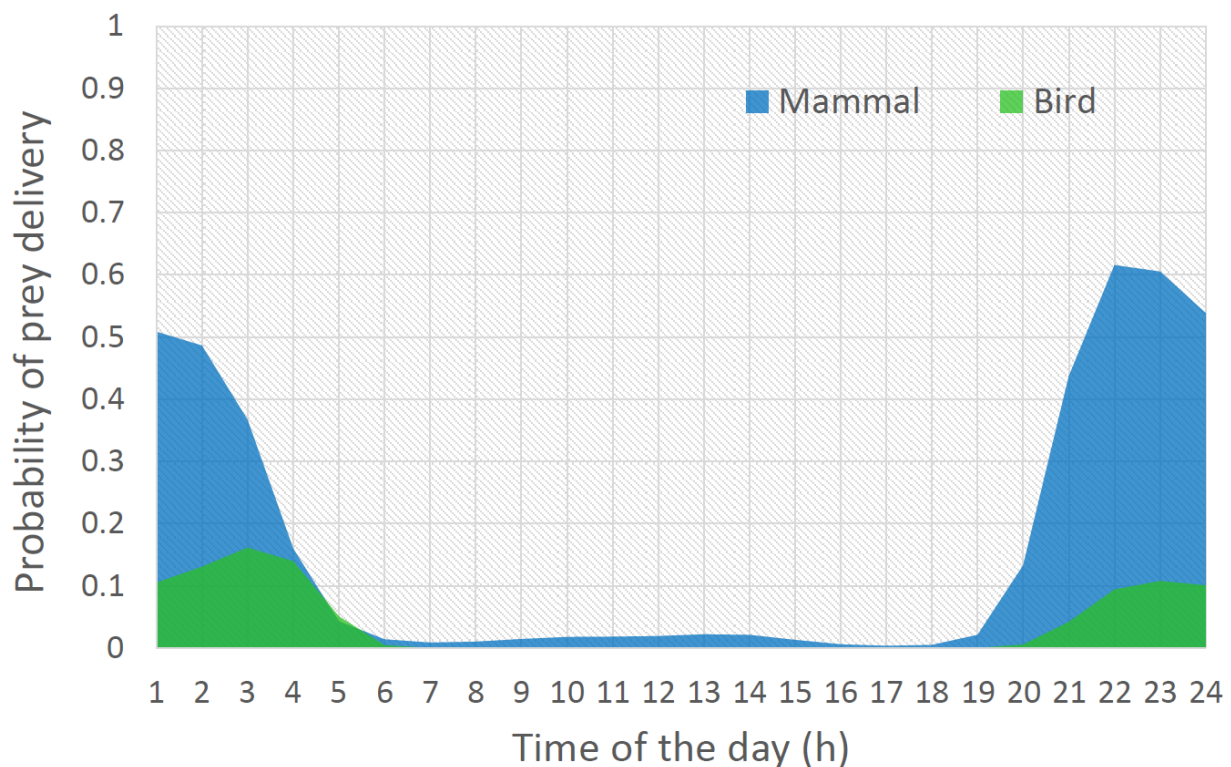


Figure 2: Probability of at least one prey delivery of a mammal (blue), and at least one delivery of a bird (green), per hour block to a tawny owl (*Strix aluco*) nest as a function of time of day, predicted from models of circadian activity rhythms. The value for hour (n) concerns the time interval from hour n to hour $n+1$.

3.1.2 Mammalian prey delivery

The models show a clear pattern of nightly deliveries of mammalian prey, where the probability of any mammalian prey was elevated between 20:00 h and 06:00 h. The wood mouse (*Apodemus sylvaticus*) showed the largest difference in probability of being delivered between evening and morning, and was also the most likely prey species to be delivered overall (Figure 3). The probability of a wood mouse delivery peaked between 22:00 h and 23:00 h with 0.32, and dropped to a lower probability for the rest of the night (Figure 3). The field vole (*Microtus agrestis*) showed a different pattern, where the probability for delivery peaked at 0.16 around solar midnight, between

24:00 h and 02:00 h. The only species of the small mammals showing two, equally distinct peaks of being delivered was the bank vole (*Myodes glareolus*), with 0.17 between 23:00 h and 24:00 h, and another peak of 0.13 between 03:00 and 04:00 h (Figure 3). The common shrew (*Sorex araneus*) clearly had the highest probability of being delivered in the evening, with a peak of 0.17 between 22:00 h and 23:00 h (Figure 3). The two specimens of mountain hare (*Lepus timidus*) and the unidentified small mammals delivered were not included in this test.

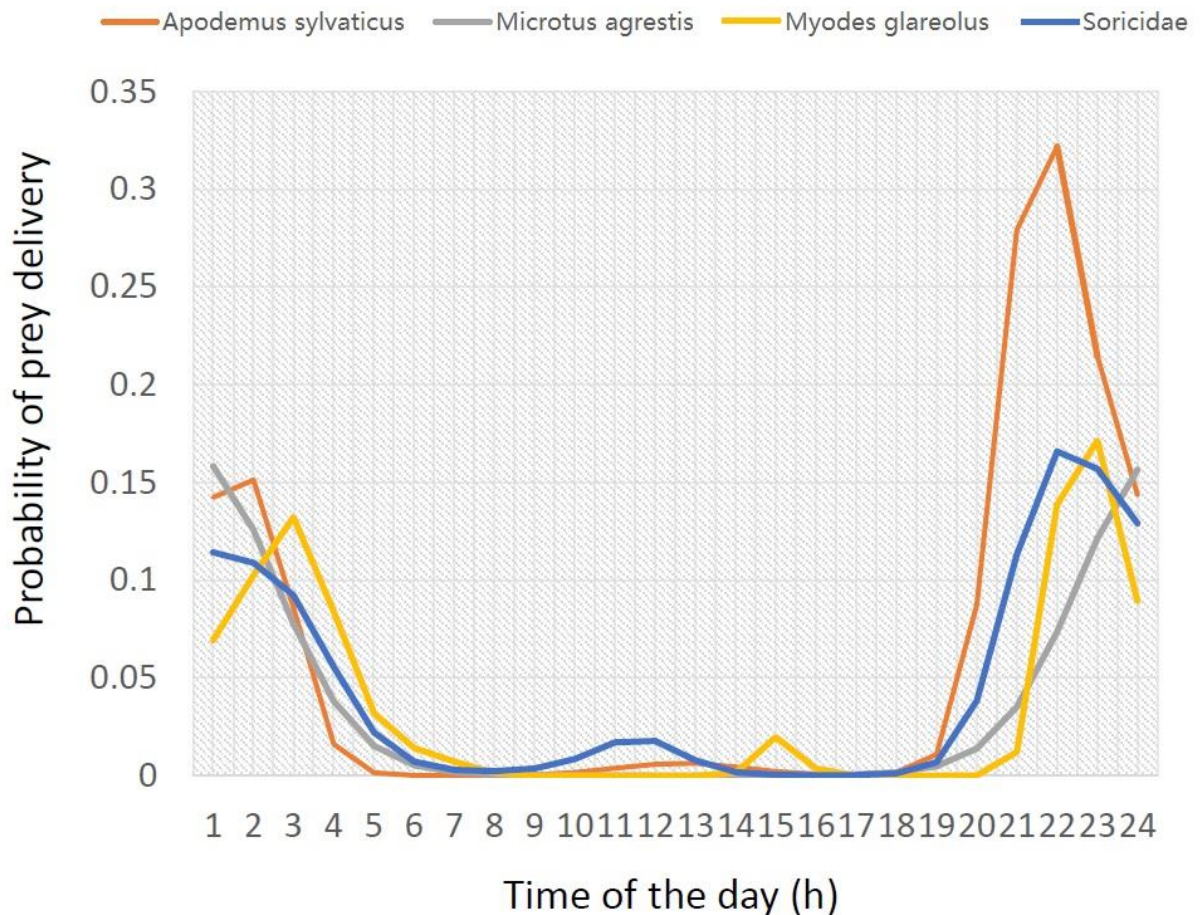


Figure 3: Probability of at least one prey delivery per hour block to a tawny owl (*Strix aluco*) nest as a function of the time of day for wood mouse (*Apodemus sylvaticus*), field vole (*Microtus agrestis*), bank vole (*Myodes glareolus*) and shrews (*Soricidae* sp.), as predicted from models.

3.1.3 Avian prey delivery

The avian prey delivered at the tawny owl nests were divided into two groups, consisting of thrushes (*Turdidae*) and other passerine birds (*Passeriformes*). The prey items of these two groups

were further divided in two, one part consisting of the adult birds and the other consisting of juvenile birds (nestlings and fledglings). Non-passerine avian prey were few, and therefore not included in this analysis. Whether the delivered avian prey was a thrush or another passerine was significantly affected by the interaction between time of day (before or after solar midnight) and whether the delivered bird was an adult or a juvenile (Table 2). The probability of delivery of a thrush rather than another passerine was higher after solar midnight than before for adults, and higher before solar midnight than after for juveniles. Other passerine birds showed an opposite pattern, where the chances of a delivery of another, adult passerine bird was higher before solar midnight than after (Figure 4).

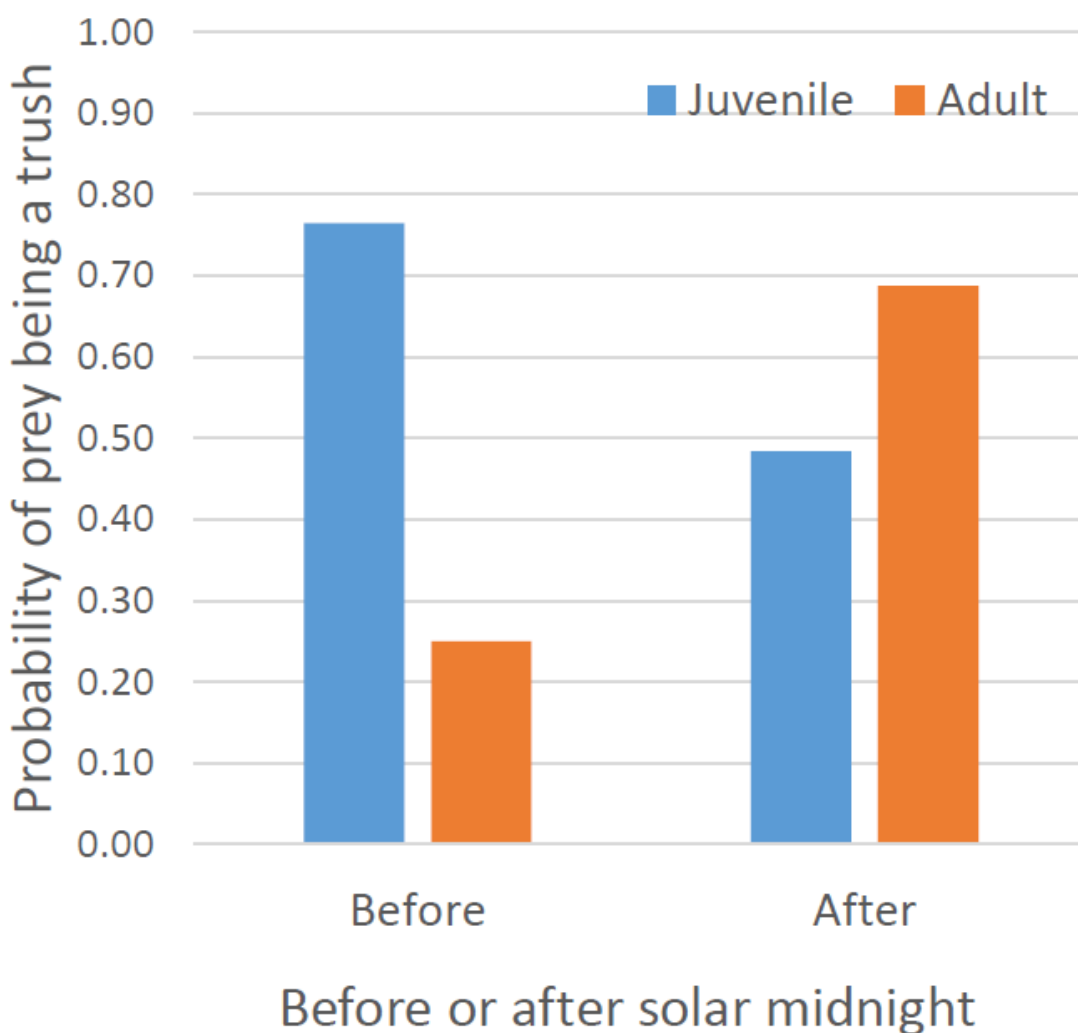


Figure 4: Probability of a prey delivered being a thrush (*Turdidae*) rather than another passerine (*Passeriformes*) as a function of if it being delivered before or after solar midnight, and whether it was a juvenile (blue, includes nestlings and fledglings) or adult (orange) at a tawny owl (*Strix aluco*) nest, and as predicted from models.

Table 2: Parameter estimates for the model of a prey item delivered being a thrush or another passerine bird, and whether the prey was a juvenile or adult (JA), as a function of before or after solar midnight (BA). Number of observations: 395, 4 nests.

	Estimate	SE	Z-value	p-value
Intercept	0.789	0.539	1.46	0.14
Time before or after solar midnight (BA)	-1.887	0.790	-2.39	0.07
Juvenile or adult (JA)	-0.853	0.648	-1.31	0.19
BA * JA	3.130	1.039	3.01	0.0026

3.1.4 Prey delivery according to nestling age

The probability that a delivered prey was a shrew rather than another prey type decreased significantly (Table 3), and the probability of a delivered prey was a bird rather than another prey type increased as the tawny owl nestlings became older (Table 4). The probability that the delivered prey was a shrew rather than another prey type was 0.35 at the start of the observation period, and dropped to less than 0.05 at the end. In contrast, the probability that the prey was a bird rather than another prey type was 0.02 in the start, and increased as the nestling became older to more than 0.50 at the end of the observation period (Figure 5). There was no corresponding, significant relationship for the other prey types.

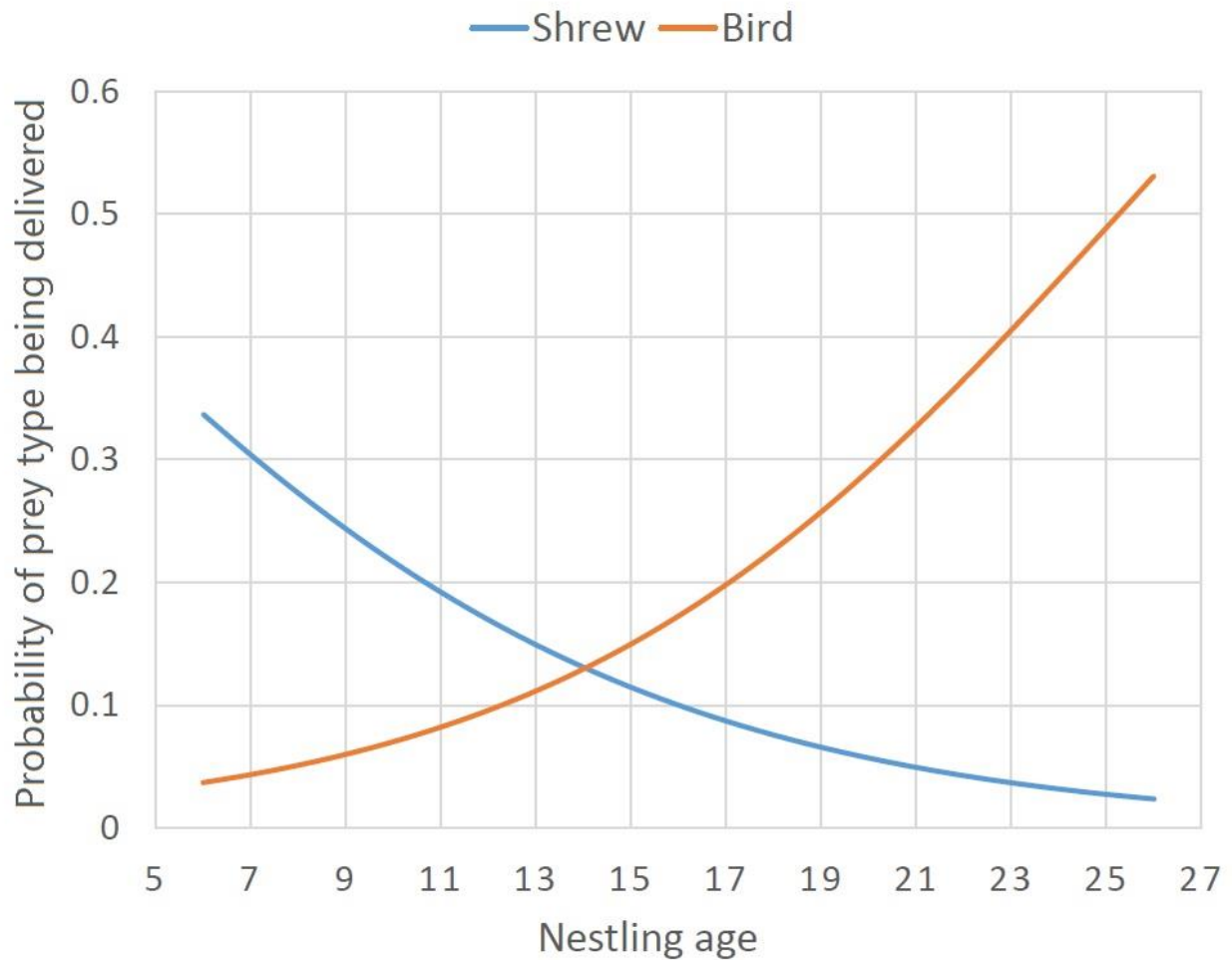


Figure 5: Probability of a prey delivered being a shrew (*Soricidae*) rather than another prey (blue line) and a bird rather than another prey (orange line), at a tawny owl (*Strix aluco*) nest, as a function of nestling age, and as predicted from models.

Table 3: Parameter estimates for the model of a prey delivered being a shrew rather than another prey type as a function of nestling age, corrected for nest ID. Number of observations: 494, 4 nests.

	Estimate	Std. error	z value	Pr (> z)
Intercept	0.235	0.451	0.52	0.603
Age	-0.152	0.030	-5.09	> 0.0001

Table 4: Parameter estimates for the model of a prey delivered being a bird rather than another prey type as a function of nestling age, corrected for nest ID. Number of observations: 506, 4 nests.

	Estimate	Std. error	z value	Pr (> z)
(Intercept)	-4.27161	0.93682	-4.56	> 0.0001
Age	0.16908	0.03237	5.223	> 0.0001

3.1.5 Prey delivery according to season

The probability that a prey item was a bird rather than another prey type increased significantly with the date, as seen in Figure 6 (Table 5). In the start of the observation period, the probability that a prey delivery was a bird was 0.02, whereas by the 23rd of May, the probability had increased to 0.35 (Figure 6). When a prey delivery was scored as a bird or another prey type, the model with season (date) as the explanatory variable was better than the model with nestling age as the explanatory variable ($AIC_c=379.92$ vs. $AIC_c=382.71$), whereas the opposite was the case when prey delivery was scored as a shrew rather than another prey type ($AIC_c=407.55$ vs. $AIC_c=425.13$).

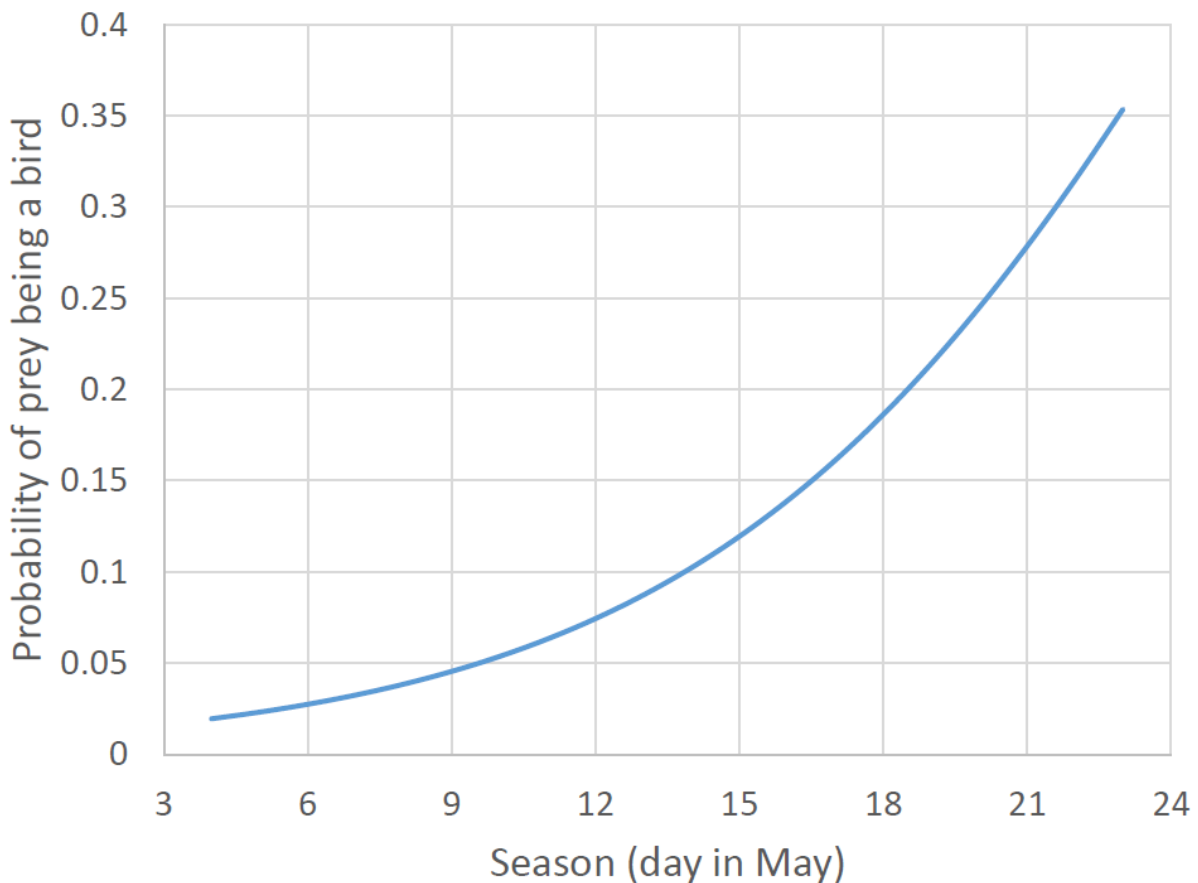


Figure 6: Probability of prey delivered at a tawny owl (*Strix aluco*) nest being a bird rather than another prey type, as a function of season, and as predicted from models.

Table 5: Parameter estimates for the model of a prey delivered being a bird rather than another prey type as a function of season, corrected for nest ID. Number of observations: 506, 4 nests.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-4.613	0.819	-5.63	> 0.0001
Season	0.174	0.032	5.407	> 0.0001

3.2 Prey handling

3.2.1 Prey handling before delivery

Only seven prey in total were registered as decapitated when delivered at the tawny owl nests. Still, there was a significant relationship between the probability of a prey being decapitated and the prey size, and the probability of a prey being decapitated increased with prey mass (Figure 7, Table 6). Only one small mammal was delivered decapitated, whereas six birds were delivered decapitated.

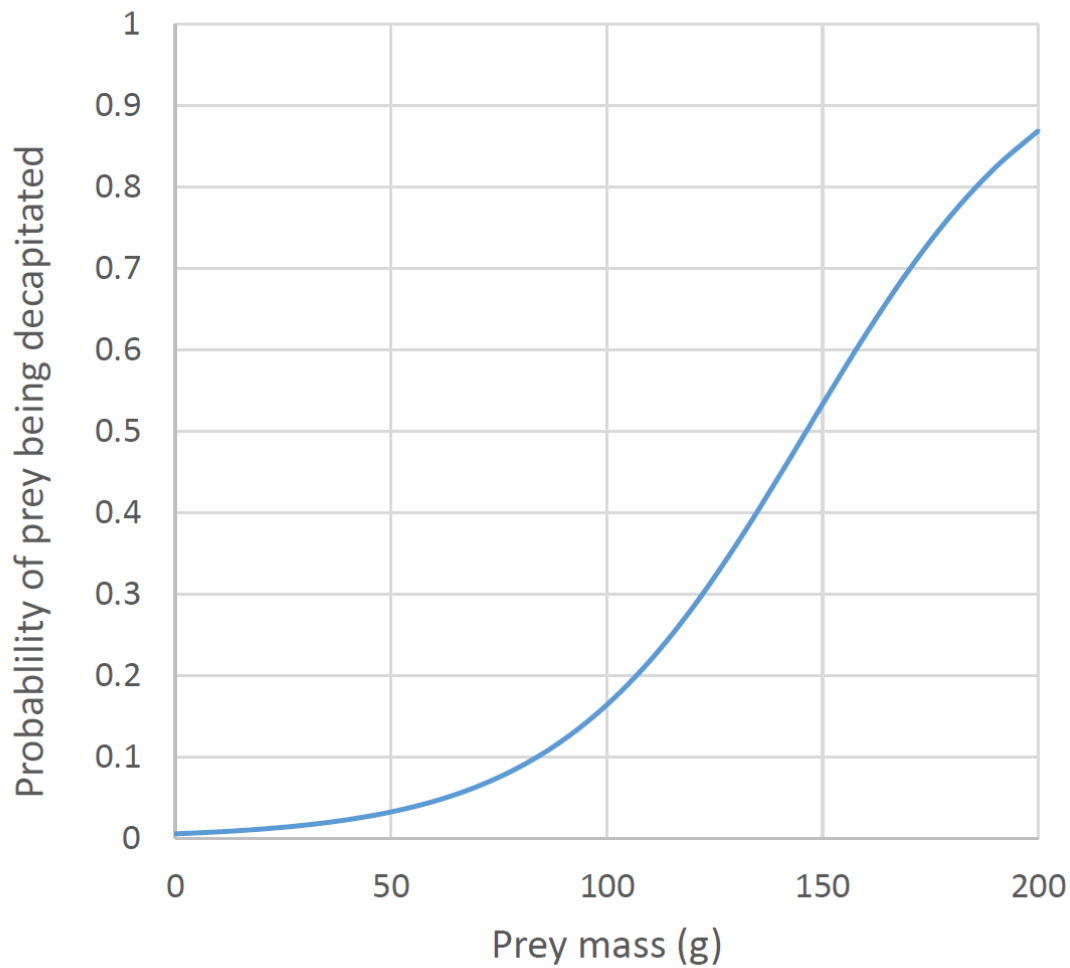


Figure 7: The probability that a prey item was delivered decapitated at a tawny owl (*Strix aluco*) nest as a function of prey body mass, and as predicted from models.

Table 6: Parameter estimates for the model of a prey delivered being decapitated upon delivery as a function of prey mass. Number of observations: 395, 4 nests.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-5.150	0.728	-7.07	< 0.0001
Prey body mass	0.352	0.012	2.85	0.0044

3.2.2 Prey handling in the nest

The tawny owl nestlings' need for assisted feeding increased with the body mass of the prey, and decreased with the nestling age (Figure 8, Table 7). The nestlings were able to ingest most of the smaller prey items unassisted from the beginning of the observation period. Shrews in particular were easily ingested, along with smaller individuals of rodents. Amphibians and insects were also mostly ingested unassisted. Often being the prey type with the largest body mass, birds were most likely to evoke feeding assistance from the female. However, the need for assistance with avian prey depended on the body mass of the bird. Nestlings, young birds and smaller bird species were ingested with less assistance than larger birds (Figure 8).

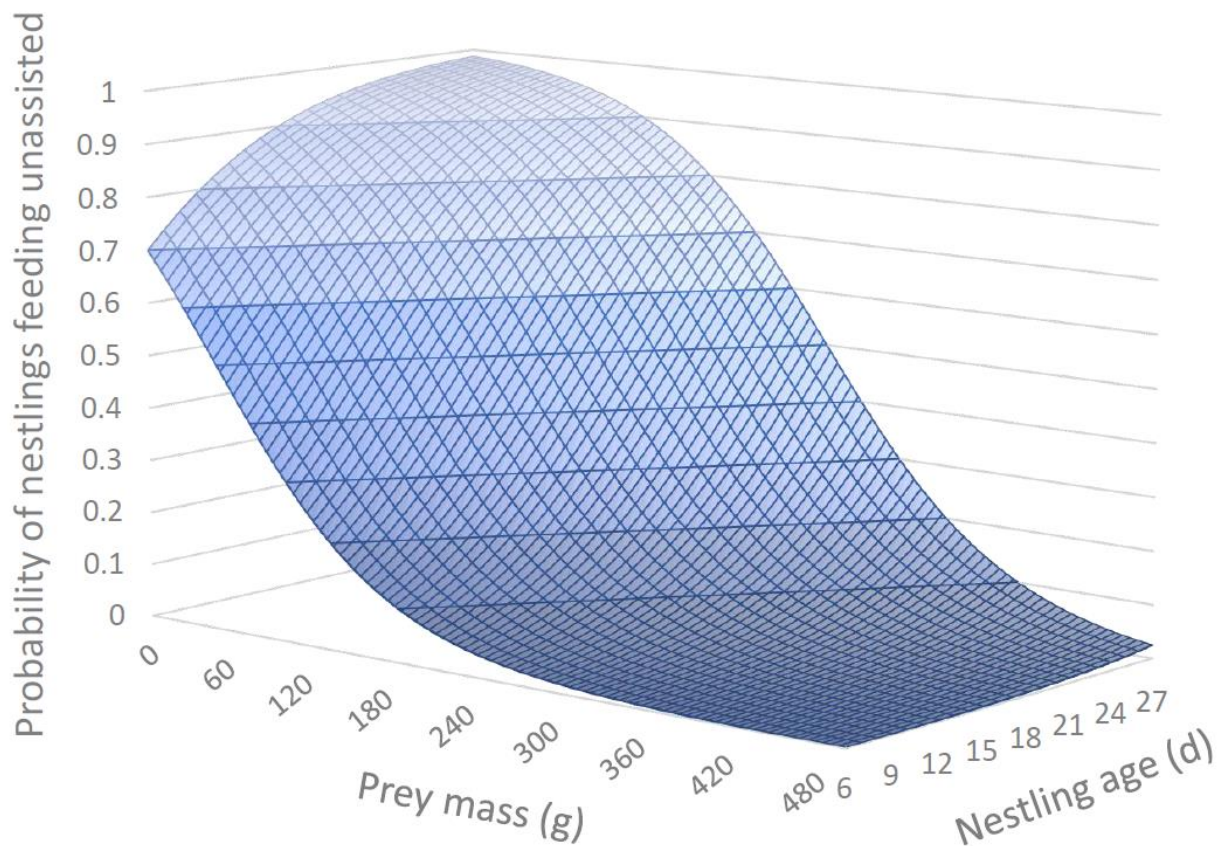


Figure 8: Probability of tawny owl (*Strix aluco*) nestlings ingesting prey unassisted rather than being fed by the female, as a function of prey mass and nestling age, and as predicted from models.

Table 7: Parameter estimates for the model of a prey item being ingested unassisted by the tawny owl nestlings rather than being fed by the female, as a function of prey body mass and nestling age, corrected for nest ID. Number of observations: 506, 4 nests.

	Estimate	Std. error	z value	Pr (> z)
Intercept	0.14	0.537	0.27	0.784
Mass	0.016	0.006	2.71	0.0067
Nestling age	-0.166	0.033	-4.99	< 0.0001

3.3 Prey mass delivered

There was a significant relationship between the mass of prey per nestling delivered at the nest each day, and the age of the nestlings (Figure 9). According to the fitted linear regression, the prey mass consumed per nestling increased throughout the observation period, with a peak around 80 g per nestling per day (Table 8). The non-linear model did not fit as well as the linear one, but was also significant (Table 9). The non-linear regression showed a peak when the nestlings were 16-17 days old. The nestlings fledged at an age of 23 days in average, although the nestlings ranged in age from 18 to 28 days at fledging.

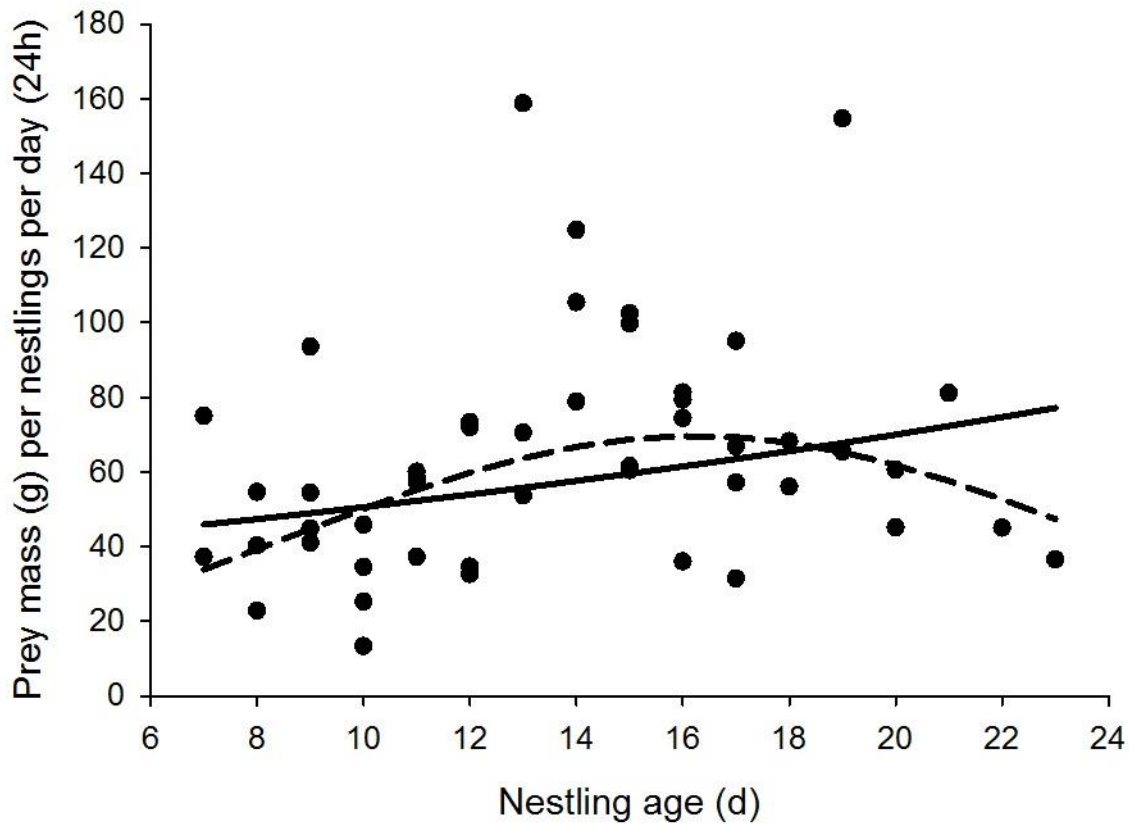


Figure 9: Prey mass (g) consumed per tawny owl (*Strix aluco*) nestling per day (24 h) as a function of nestling age in days, shown as a linear model (black line) and a non-linear model (hatched line), as predicted from models.

Table 8: Parameter estimates for the linear model of prey mass being ingested per nestling per day (24h), as a function of nestling age. Number of observations: 48, 4 nests.

	Estimate	Std. error	t-value	p-value
Intercept	1.562	0.102	15.30	0
Age	0.014	0.007	1.98	0.0537

Table 9: Parameter estimates for the non-linear model of prey mass being ingested per nestling per day (24h), as a function of nestling age. Number of observations: 48, 4 nests.

	Estimate	Std. error	t-value	p-value
Intercept	0.875	0.307	2.85	0.0068
Age	0.119	0.045	2.64	0.0115
I (age ²)	-0.004	0.002	-2.36	0.0232

4. DISCUSSION

4.1 *Choice of prey*

The prey items delivered to the tawny owl nestlings were by number, 66% mammalian, 18% avian, 5% amphibian, 5% invertebrate and 0.5% reptilian. In addition, 5% of the prey items could not be identified. The mammalian prey delivered were, by number, 41% wood mouse, 24% shrews, 14% field vole and 13% bank vole. Also, mammalian prey was the largest prey group in terms of biomass, constituting 60% of the total delivered prey mass. Wood mouse was the most delivered prey overall, with 145 individuals in total. Based on the time of deliveries, the tawny owls were mainly nocturnal hunters, collecting most of their prey between sunset and sunrise. The majority of prey were delivered to the nest at night, although a few deliveries occurred during the daytime. The hour blocks with the highest probability for prey delivery overall was between 22:00 and 23:00 h, i.e. around 2 hours after sunset, but 2-3 hours before solar midnight.

4.1.1 *Mammalian prey delivery*

The probability that a wood mouse was the prey brought to the nest peaked at 0.32 between 22:00 h and 23:00 h. For the bank vole, the probability of delivery peaked twice a day. The first peak occurred from 23:00 h to solar midnight, and the other between 03:00 h and 04:00 h. The field vole had the highest probability of being brought to the tawny owl nest the last hour before solar midnight.

The population level for voles at a given year has a close connection to breeding success in raptors that prey on voles (Sundell et al. 2004; Millon et al. 2014). The field vole is considered the main prey type of the tawny owl in most habitats (e.g. Millon et al. 2014), so the high amount of wood mouse compared to field voles recorded in my study differs from what has been found in earlier research. Petty (1999) found that field voles were the most hunted prey by the tawny owl with 62% of all prey items in coniferous forest in England, whereas the wood mouse only contributed with 3% of delivered prey. This is also in line with what Lundberg (1980) found in Sweden, where in a top year, the field vole contributed with 40% of prey items identified from pellets. When the field vole population decreased in the following year, the water vole became the most important prey with 33% (Lundberg 1980). Lundberg found that the wood mouse increased from 7% to 12% of

total prey in the same years, which may indicate that the wood mouse is not the preferred prey type for the tawny owl, but an alternative one. An experiment done in Finland suggested that the field vole is diurnal in winter and nocturnal in summer (Erkinaro 1961), and showed that the activity pattern of the field vole shifted in May. It had the highest activity level at 00:00 hours, and between 00:00 and 02:00 hours in the end of May (Erkinaro 1961). This fits with my results. Another study suggests that the field vole has bursts of nightly activity periods in summer, and only leaves the nest for necessary food and water during daytime in this season (Lehmann 1976). The relatively low amount of field vole captured in my study may be explained by the population levels of the mammal. Compared to the bank vole, the field vole constituted only 1% of small mammals captured by long-term snap trapping near my study area (Geir A. Sonerud pers. comm.). In addition, the tawny owl preferred to hunt in deciduous forest in my study area, as shown by radio telemetry (Eldegard 1996), whereas the field vole mostly occurred in open areas (Geir A. Sonerud pers. comm.).

The tawny owl switches to alternative prey types when the populations of the preferred prey types are low (Solonen & Karhunen 2002). Nishimura & Abe (1988) tested the attack frequency and hunting efficiency of the Ural owl (*Strix uralensis*) on species of the *Apodemus* and *Microtus* genus. The Ural owl and the tawny owl share several similarities and has overlapping niches (Korpimäki 1986a), making the results transferable. Nishimura & Abe (1988) found that the Ural owl did not discriminate between prey types when attacking, but had a much higher success chance of capturing a *Microtus* vole than a *Apodemus* mouse. In addition, Zárbynická et al. (2013) found a positive correlation between the availability of the *Apodemus* mouse and the hunting frequency in the Tengmalm's owl (*Aegolius funereus*) in the Czech Republic. This correlation was not found for the *Microtus*, even though the latter constituted a bigger part of the Tengmalm's owl diet (Zárbynická et al. 2013). Another explanatory part may be the population levels of rodents. Based on long-term trapping of small mammals near my study area, the bank vole and the wood mouse had peak populations in my study year (Geir A. Sonerud, pers. comm.). If one assumes that what Nishimura & Abe (1988) found also applies to the tawny owl, the wood mouse may have been the most accessible prey in the tawny owl territories at the time, and was therefore caught with the highest frequency, even with a reduced chance of a successful catch.

Southern & Lowe (1968) found that the wood mice were usually evenly distributed in a tawny owl territory, whereas the bank vole preferred denser cover and therefore had a more selective distribution. The tawny owl alters flight technique according to vegetation type (Nilsson 1978), but

avoids open space, including grasslands, crops and clear cuts (Eldegard 1996). The wood mouse mostly occur in deciduous forest (Geir A. Sonerud pers. comm). It may also play into part that the wood mouse is mainly nocturnal, while the bank vole can be active at all times of the day (Southern & Lowe 1968). However, Greenwood (1978) found that 87% of bank vole activity happened at daytime in the summer, with activity peaks around sunrise and sunset. In Scotland, the wood mouse favours a long, consecutive activity period between 22:00 h and 02:00 h in late spring and summer, with the exception of females with litters (Wolton 1983). In a field experiment in England, Greenwood (1978) found no wood mouse activity during the daylight hours, confirming the species to be nocturnal.

Shrews were second only to the wood mouse in numbers delivered at the tawny owl nests, with 86 prey items recorded. The probability of delivery of shrews peaked in the evening between 22:00 h and 23:00 h, and also had a small increase in probability around midday. Experiments done by Churchfield (1982) in England showed a higher activity level at night than during daytime, but also showed activity periods during both day and night in summer temperatures. Research done in Poland confirmed this, and also states that activity related to both foraging and general movement increases during summer months (Buchalczyk 1972). The seemingly random activity pattern that are common for shrews may explain the small daytime probability peak, as the prey can be available at all times of the day.

Cramp (1985) stated that the tawny owl adjusts its diet to the prey species found in its territory, and utilizes what is available in the given area. Because the tawny owl is an opportunistic generalist (Lambin et al. 2000), the availability of mammalian prey seems to play a major part in the choice of prey by the tawny owl. The amount and type of small mammals that is present in the tawny owl territory is not only dependent on forest type, but also on amount of ground cover, which again reflects on the choice of prey (Southern & Lowe 1968; Balčiauskienė et al. 2005). Territorial mapping and vegetation mapping was not done for the tawny owl territories in my study, but the areas mainly consist of a combination of forest patches and agricultural areas (see chapter 2.1).

4.1.2 Avian prey delivery

The probability of delivery of avian prey for every hour block was lower than the probability of delivery of mammalian prey around the clock in my study. The probability of one or more avian

prey deliveries peaked between 03:00 h and 04:00 h with 0.16. In the evening, the probability increased to 0.10 from 22:00 h. Birds were the second largest prey group after mammals, making up 18% of prey deliveries. Among adult birds, thrushes had a higher probability than other passerines of being delivered after solar midnight than before, whereas among nestlings and fledglings being delivered, thrushes were more likely to be delivered before solar midnight than after.

Birds are commonly considered an alternative prey for the tawny owl (Jędrzejewski et al. 1994). However, the owls have a high adaptability to the prey types available (Cramp 1985). For example, birds have been shown to constitute a more important part of the tawny owl diet in urban areas, compared to suburban and woodland areas (Zalewski 1994). In some areas, birds can even be considered as the main prey type for the tawny owl, depending on the abundance of other prey types (Cramp 1985).

Even though the “sit-and-wait” tactic is the most common hunting method of the tawny owl, it is able to adjust the hunting method to the prey type available (Cramp 1985). When hunting for avian prey, the tawny owl is known to catch roosting birds (Harrison 1960), and will use methods such as hovering, diving and sound-making with its wings to drive avian prey out from hiding (Cramp 1985 and references therein). It will also pick unfledged birds from nests (Schaefer 2004). I observed that several nestlings of the same species and apparent age were delivered to the tawny owl nests in succession. Avian predators often return to the same prey nest several times, collecting all available prey (Sonerud 1985; Weidinger 2010). In addition, one of the more common avian prey species from my study, the fieldfare (*Turdus pilaris*), often nests in colonies (Götmark et al. 1995). One would assume that upon the discovery of such a colony, the tawny owl would return to raid several nests in succession, given that the risk of being mobbed is not too high (Sunde et al. 2003).

Birds alter their activity patterns in different ways when exposed to avian predation (e.g. Suhonen et al. 1994). Some bird species will spend the whole day feeding when exposed to predation risk; Bonter et al. (2013) recorded that passerines showed foraging activity from before sunrise until approximately 2 hours before sunset when predation was imminent. Singing patterns may also be altered; Slagsvold et al. (1994) found that some males of the great tit (*Parus major*) increased their singing activity when the female was at the nest and predators were nearby. Great tits have also shown to modify both their sleep pattern and behavior during the day when exposed to avian predation (Stuber et al. 2014). Birds reduced their time in slow-wave sleep and were more sensitive to disturbances when exposed to predators, especially the prey species that sleep in open areas

(Roth et al. 2006). In addition, the sound of owl hooting may reduce the amount of singing after dusk in the veery (*Catharus fuscescens*), an American thrush (Schmidt & Belinsky 2013).

Nighttime vocalization by diurnal birds has been shown in a large number of avian species (La 2012). In addition, diurnal bird song has been thoroughly recorded in my study area. In springtime, the thrushes start to sing only a few hours after solar midnight, and are active far into the evening (Geir A. Sonerud pers. comm.). Most other passerines are less nocturnal, and start singing half an hour before sunrise (Geir A. Sonerud pers. comm.). The retinal structure of thrushes seems to give them good vision in dark conditions, which may explain their semi-nocturnal singing (McNeil et al. 2005). When studying bird song in Norway, Slagsvold (1977) found two seasonal periods with distinct peaks in diurnal singing activity. The first peak occurred in early spring before egg laying, the other peak occurred in May, around fledging time (Slagsvold 1977). This may indicate that my study was done during a period where bird song was frequent. As the tawny owl uses its hearing to localize prey (Cramp 1985), bird song occurring during the tawny owl's active period may lead the raptor to its prey.

The higher nocturnal song activity in thrushes than in other passerines provides an explanation of the high probability of thrushes relative to other passerine birds being delivered in the very early morning in May. If this is the case, the prey delivery time of the tawny owl may closely reflect the diel activity patterns of the avian prey.

4.1.3 Prey delivery according to nestling age

The probability that the delivered prey was a shrew rather than another prey type was fairly high when the nestlings were young, and declined throughout the nestling period. In opposite, the probability of delivery of avian prey was very low in the beginning of the season and increased steadily. In addition, smaller prey were easier to consume unassisted for the nestlings at a low age. Larger prey from the size of a field vole and upwards needed to be prepared prior to feeding during the first days of recording, as the nestlings seemed too small to be able to swallow such prey whole. However, the nestlings were able to swallow most shrews whole from the beginning of the filming period. The average body mass of shrews was 10 g, which is about half the mass of any other mammalian prey type delivered at the tawny owl nests.

In contrast to my findings, Steen (2010) found that delivery of larger prey was more efficient in the beginning of the nestling period for common kestrels (*Falco tinnunculus*), as the nestlings needed prey preparation for prey of all sizes anyway. When the nestlings became older, a shift to smaller prey would pay off, as the nestlings would be able to swallow such prey whole (Steen 2010). The kestrel has a smaller average size than the tawny owl. The average size of an adult, male kestrel is about 200 g (Sonerud et al. 2013), whereas the male tawny owl weighs about 400 g (Cramp 1985). This may imply a higher swallowing capacity in the tawny owl nestlings than in the common kestrel nestlings, and therefore an ability to consume larger prey without preparation. In addition, Slagsvold & Sonerud (2007) found a negative relationship between prey size and ingestion rate in raptors, deeming it more profitable to hunt smaller prey types. The preparation time for smaller prey was lower, which may increase the available time to hunt (Slagsvold & Sonerud 2007). This may explain the high amount of shrews over the first few weeks of my observation period, making it the most efficient prey type for the young nestlings. However, as the nestlings grew, the need for higher amounts of prey mass would increase (Slagsvold & Wiebe 2007), which may be why the amount of avian prey increased during the observation period. The size difference between the kestrel and the tawny owl may account for the contrasting results from my study and that of Steen (2010).

4.1.4 Prey delivery according to season

There was a significant correlation between the date and the selection of birds over other prey types in the tawny owl. My study was conducted in May, and the increasing probability of avian prey continued throughout the month. Kirk (1992) found that the tawny owl shifted from mainly mammalian to more avian prey during the breeding season, and found that birds contributed 69% of total food intake between April and August. In addition, Newton (1979) stated that the populations of small birds increases in spring, and that the seasonal changes in food intake by many raptors is determined by changes in prey abundance.

In the post-fledgling period of a bird, there is a high risk of predation in most avian species (Naef-Daenzer et al. 2001). For example, only 19% of fledgling hooded warblers (*Wilsonia citrina*) survived to adulthood in the USA (Rush & Stutchbury 2008). Similarly, Magrath (1991) found juvenile blackbirds (*Turdus merula*) to be at their most vulnerable during the fledging period in England. Thrushes nest between April and June in Scandinavia (Götmark et al. 1995). The increased availability of vulnerable avian prey in the breeding season seems to benefit the tawny

owl. High availability of nestlings and fledglings may account for some of the increasing amount of avian prey throughout the season in my study.

4.2 Prey handling

4.2.1 Prey handling before delivery

The adult tawny owls did not do any prey preparation on any of the small mammal items except one in prior to delivery at the nest, whereas six of the avian prey items were decapitated upon delivery. However, overall probability of decapitation increased with prey mass, which corresponds to that found for other avian species. Kaspari (1990) found that the amount of prey preparation increased with the prey size in adult grasshopper sparrows (*Ammodramus savannarum*), whereas Steen et al. (2010) found the same for prey fed to common kestrel nestlings. Moen (2014) also found that the probability of prey handling decreased with the age of the nestlings and increased with the size of prey in the Ural owl. Prey preparation may enhance the success chance of reproduction, as it enables the parents to hunt larger prey for the nestlings, while bypassing the size limitations in the swallowing capacity of the nestlings (Rands et al. 2000).

In common kestrels, Steen et al. (2010) found that decapitation was less likely when the nestlings were older, and more likely for avian than mammalian prey. However, nestling age could not be taken into account when prey handling was analyzed in my study, due to a too small sample of decapitated prey items. In addition, several of the prey items in my study were not scored as decapitated or not, because speedy prey deliveries or nestlings moving between the camera and the prey rendered some of the prey heads undistinguishable. Therefore, some cases of decapitation may have passed unnoticed in my study. In some cases, the parents left larger prey in the nest box, seemingly to encourage the nestlings to prepare the prey themselves. When they were not able to, the female would enter the nest box at a later time and help with the prey preparation. In these cases, decapitation may have occurred after the delivery. Hence, my data set might be too small to conclude firmly on decapitation, other than provide the observation that tawny owls do not decapitate small prey types very often in prior to feeding their nestlings.

4.2.2 Prey handling in the nest

Both prey body mass and nestling age affected the nestlings' ability to ingest the prey without assistance from the female. The nestlings were in need of more assistance when they were younger and when the prey was larger. In addition, the smaller prey items were less often prepared in terms of decapitation than the larger prey. Shrews were never prepared in any way, and larger birds were sometimes decapitated or plucked. Similar results were obtained for the Ural owl by Rønning (2007).

My results are in line with the feeding constraint hypothesis, which states that due to size and age difference in the nestlings, the need for prey preparation increases with the size of prey (Slagsvold & Wiebe 2007). This is because smaller nestlings are less able to ingest larger prey items than their larger siblings (Slagsvold & Wiebe 2007). When the food demand increases as the nestlings grow, the parents will hunt larger prey that is more efficient, and if the parents does not provide necessary feeding assistance or smaller prey to the younger nestlings, their survival chance decreases (Slagsvold & Wiebe 2007). Steen et al. (2010) found a decrease of prey preparation rate of voles with increased nestling age in the Eurasian kestrel, but no such relationship for birds, which was believed to be related to the large size of most avian prey, which would need to be prepared regardless of the nestling age (Steen et al. 2010). Similar results were obtained by Slagsvold & Wiebe (2007) for the pied flycatcher (*Ficedula hypoleuca*). In addition, broods with nestlings of different age were provided with significantly larger prey than broods with nestlings of the same age, which reduced the survival chance of the younger nestlings (Slagsvold & Wiebe 2007). Tawny owl nestlings hatch asynchronously (Hardey et al. 2006). In a brood size of five nestlings, as in nest box K3, this may give an age difference of more than a week between the youngest and oldest nestling.

However, there seemed to be an exception to the pattern. In nest box K1, the female seemed to be “purposely” giving the prey items to the smallest nestling, pushing the other nestlings out of the way to make sure the smallest one was fed. There was also a large number of shrews being delivered at this nest (Appendix 2). Most of the shrews were fed to the smallest nestling. This behavior continued until the nestling was as large as its siblings. There were originally four nestlings in K4, and all survived. This pattern was not observed in any of the other nest boxes, where the parental feeding pattern seemed to follow the feeding constraint hypothesis, and the size difference among the nestlings grew over time. This exception with selective allocation of small

prey to the smallest nestling could be interesting to follow up in future research.

4.3 Prey mass delivered

According to the linear model, the mass of prey delivered increased throughout the observation period. The less likely non-linear model showed a peak in prey mass delivered when the nestlings were estimated to be 16-17 days old. Some raptors seem to adjust the prey mass delivered to the age and needs of the nestlings (Steen et al. 2012). According to Percival, cited in Hardey et al. (2006), the growth of tawny owl nestlings levels off when the nestlings are 32-33 days old, while Cramp (1985) stated that the tawny owl parents provided the largest amount of food when the nestlings were 11-25 days old. The average fledging age in my study was 23 days. However, average fledging age in England was found to be 32 days in a year with a low vole population (Coles & Petty 1997). In Denmark, Sunde (2008) observed that the nestlings fledged when 34 to 39 days old. This may indicate a miscalculation of the average fledgling age in my study. Indeed, the fledgling age in my study was based on the youngest nestling in each clutch. The tawny owl nestlings hatch asynchronously (Hardey et al. 2006), which means that the oldest nestling may be up to a week older than the youngest individual. If this is the case, the age of the oldest fledgling at fledging would fit with the results obtained by others.

The parents provided an average of 57 g per nestling per day (24 hours), which is equivalent of about two field voles. This is in line with Cramp (1985 and references therein) who reports an average delivery of 2-4 prey per nestling per day. Sasvári et al. (2000) found that the prey delivered by the tawny owl parents increased with the number of nestlings in the brood. Thus, one can assume that the workload of the parents depends on the number of nestlings. If that is the case, in nest box K2 with only three hatched nestlings, the parents would have needed to provide an average of 171 g of prey mass per day, which equals about 7 wood mice or about 17 shrews. In nest box K3 with five nestlings, the daily need would equal 285 g, which is equivalent to 11-12 wood mice, or 28-29 shrews. This underlines how a higher number of nestlings may increase the parental workload. The only observed loss of a nestling occurred in K4, which also was the only nest with five hatched nestlings. The parental workload in this nest may have been too large, compared to the other tawny owl pairs with fewer nestlings to feed.

5. CONCLUSIONS

The tawny owl delivered a wide range of prey species to the nest, confirming it to be a food generalist. The owl seemed to hunt the most available and most efficient prey type for the season and time of day. Mammalian prey were the most numerous prey group, but birds also contributed a large part of their diet. Most prey deliveries happened at night, although a few deliveries occurred in the daytime, which coincides with earlier research done on the tawny owl. The delivery time of mammalian and avian prey species could be linked to their preferred habitat type, population level and diel activity pattern. In addition, the increase in avian prey during the observation period and the probability for decapitation also seemed to be related to hunting efficiency and swallowing capacity of the nestlings. When it comes to feeding assistance inside the nest box, my results in three of the nests conform to the feeding constraint hypothesis (Slagsvold & Wiebe 2007). A comparison to earlier research revealed that my age estimates of the nestlings may have been under-calculated. However, a link could be found between the prey mass delivered and the nestling age, as the tawny owl pair seemed to adapt the prey mass to the needs of the nestlings. The selective prey allocation between nestlings in one of the nest boxes was an exciting observation that would be interesting to investigate in the future. Finally, the singing pattern of the avian prey species may also play into part in prey choice by the tawny owl. The research done on nocturnal birdsong from diurnal birds seems to be an understudied field, and more research would be needed to conclude on this subject.

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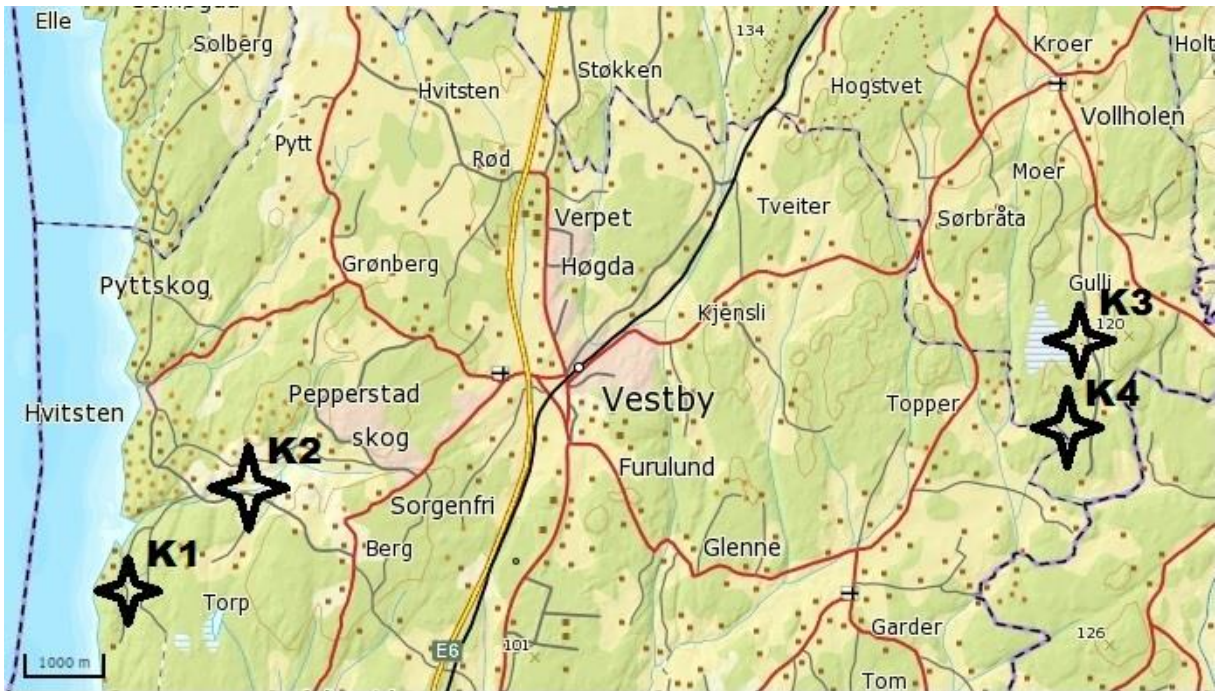
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A. APPENDIX



*Appendix 1: Map of the study area, located in Akershus county, southeastern Norway. The tawny owl (*Strix aluco*) nest boxes filmed (K1, K2, K3 and K4) are marked with stars.*

Appendix 2: Prey items delivered to the tawny owl (*Strix aluco*) nests as recorded by video, sorted by nests (K1, K2, K3 and K4).

Species	K1	K2	K3	K4	Total
Common shrew (<i>Sorex araneus</i>)	36	4	33	12	85
Eurasian water shrew (<i>Neomys fodiens</i>)	0	0	1	0	1
Mountain hare (<i>Lepus timidus</i>)	2	0	0	0	2
Bank vole (<i>Myodes glareolus</i>)	20	10	9	7	46
European water vole (<i>Arvicola amphibious</i>)	0	1	3	0	4
Field vole (<i>Microtus agrestis</i>)	10	6	20	13	49
Unidentified Cricetidae	1	1	1	2	5
Wood mouse (<i>Apodemus sylvaticus</i>)	77	47	18	3	145
Unidentified small rodent	3	0	2	0	5
Unidentified small mammal	8	0	1	0	9
Mammals, total	157	69	88	37	351
Common moorhen (<i>Gallinula chloropus</i>)	0	0	0	1	1
Common wood pigeon (<i>Columba palumbus</i>)	1	0	0	0	1
Eurasian pygmy owl (<i>Glaucidium passerinum</i>)	0	0	1	0	1
Tree pipit (<i>Anthus trivialis</i>)	0	0	0	1	1
European robin (<i>Erithacus rubecula</i>)	1	0	0	1	2
Song thrush (<i>Turdus philomelos</i>)	0	1	2	0	3
Song thrush (<i>Turdus philomelos</i>) or redwing (<i>Turdus iliacus</i>)	1	0	1	5	7
Fieldfare (<i>Turdus pilaris</i>)	0	2	0	0	2
Common blackbird (<i>Turdus merula</i>)	0	0	1	1	2
Unidentified thrush (<i>Turdus</i> sp.)	1	0	12	22	35
Common whitethroat (<i>Sylvia communis</i>) or lesser whitethroat (<i>Sylvia curruca</i>)	0	1	0	0	1
Willow warbler (<i>Phylloscopus trochilus</i>)	0	1	0	0	1
Unidentified Sylviidae	1	1	0	0	2
European pied flycatcher (<i>Ficedula hypoleuca</i>)	0	0	0	1	1
Great tit (<i>Parus major</i>)	2	0	0	0	2
Common chaffinch (<i>Fringilla coelebs</i>)	0	0	1	6	7
Unidentified small birds	0	2	11	15	28
Birds, total	7	8	29	53	97
Slow worm (<i>Anguis fragilis</i>)	1	0	0	2	3
Frog (<i>Rana</i> sp.)	5	0	16	6	27
Earthworm (Lumbricidae)	0	0	18	0	18
Beetle (Coleoptera)	0	0	1	0	1
Carabidae (Coleoptera)	0	0	1	0	1
Grasshopper (Saltatoria)	1	0	0	0	1
Owlet moth larvae (Noctuidae)	1	0	0	0	1
Unidentified insect larvae	0	1	4	0	5
Invertebrates, total	2	1	24	0	27
Unidentified prey	17	3	3	3	26
All prey, total	189	81	160	101	531

Appendix 3: Parameter estimates for all prey, based on the probability of delivery of one or more prey items per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-2.312	0.174	-13.262	< 0.0001
I (cos(2 * pi * hour/24))	2.444	0.192	12.719	< 0.0001
I (sin(2 * pi * hour/24))	0.493	0.265	1.864	0.0623
I (cos(2 * 2 * pi * hour/24))	1.277	0.241	5.289	< 0.0001
I (sin(2 * 2 * pi * hour/24))	0.448	0.193	2.317	0.020508
I (cos(3 * 2 * pi * hour/24))	-0.203	0.214	-0.952	0.341273
I (sin(3 * 2 * pi * hour/24))	-0.383	0.224	-1.715	0.086371
I (cos(4 * 2 * pi * hour/24))	-0.666	0.181	-3.676	0.000237
I (sin(4 * 2 * pi * hour/24))	-0.466	0.179	-2.605	0.009194

Appendix 4: Parameter estimates for small mammalian prey, based on the probability of delivery of one or more mammalian prey items per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-2.834	0.293	-9.661	< 0.0001
I (cos(2 * pi * hour/24))	2.386	0.217	10.990	< 0.0001
I (sin(2 * pi * hour/24))	0.221	0.327	0.675	0.4996
I (cos(2 * 2 * pi * hour/24))	1.450	0.269	5.382	< 0.0001
I (sin(2 * 2 * pi * hour/24))	0.295	0.239	1.236	0.2166
I (cos(3 * 2 * pi * hour/24))	-0.347	0.251	-1.383	0.1668
I (sin(3 * 2 * pi * hour/24))	-0.289	0.254	-1.139	0.2546
I (cos(4 * 2 * pi * hour/24))	-0.501	0.198	-2.524	0.0116
I (sin(4 * 2 * pi * hour/24))	-0.393	0.204	-1.925	0.0542

Appendix 5: Parameter estimates for voles, based on the probability of delivery of one or more voles per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-3.383	0.339	-9.975	< 0.0001
I (cos(2 * pi * hour/24))	2.625	0.323	8.125	< 0.0001
I (sin(2 * pi * hour/24))	0.047	0.430	0.110	0.91240
I (cos(2 * 2 * pi * hour/24))	1.337	0.368	3.634	0.00028
I (sin(2 * 2 * pi * hour/24))	0.643	0.331	1.942	0.05214
I (cos(3 * 2 * pi * hour/24))	-0.193	0.354	-0.545	0.58570
I (sin(3 * 2 * pi * hour/24))	-0.316	0.339	-0.932	0.35119
I (cos(4 * 2 * pi * hour/24))	-0.660	0.252	-2.624	0.00868
I (sin(4 * 2 * pi * hour/24))	-0.529	0.248	-2.137	0.03259

Appendix 6: Parameter estimates for shrew based on the probability of delivery of one or more shrews per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-4.417	0.531	-8.321	< 0.0001
I (cos(2 * pi * hour/24))	2.114	0.384	5.509	< 0.0001
I (sin(2 * pi * hour/24))	0.805	0.592	1.361	0.173574
I (cos(2 * 2 * pi * hour/24))	1.456	0.432	3.367	0.000759
I (sin(2 * 2 * pi * hour/24))	-0.581	0.499	-1.164	0.244268
I (cos(3 * 2 * pi * hour/24))	-1.060	0.377	-2.814	0.004889
I (sin(3 * 2 * pi * hour/24))	-0.143	0.294	-0.488	0.625495

Appendix 7: Parameter estimates for bank vole, based on the probability of delivery of one or more bank voles per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-6.991	2.017	-3.467	0.000527
I (cos(2 * pi * hour/24))	4.812	2.935	1.639	0.101132
I (sin(2 * pi * hour/24))	1.601	1.204	1.329	0.183693
I (cos(2 * 2 * pi * hour/24))	-0.339	2.146	-0.158	0.874578
I (sin(2 * 2 * pi * hour/24))	1.894	1.396	1.357	0.174826
I (cos(3 * 2 * pi * hour/24))	2.183	1.622	1.346	0.178319
I (sin(3 * 2 * pi * hour/24))	-2.799	1.811	-1.545	0.122290
I (cos(4 * 2 * pi * hour/24))	-1.988	0.937	-2.122	0.033866
I (sin(4 * 2 * pi * hour/24))	0.215	0.766	0.281	0.778901

Appendix 8: Parameter estimates for field vole, based on the probability of delivery of one or more field voles per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-5.811	0.715	-8.132	< 0.0001
I (cos(2 * pi * hour/24))	4.126	0.787	5.244	< 0.0001
I (sin(2 * pi * hour/24))	0.594	0.348	1.706	0.0881

Appendix 9: Parameter estimates for wood mouse, based on the probability of delivery of one or more wood mice per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-4.871	0.791	-6.159	< 0.0001
I (cos(2 * pi * hour/24))	2.683	0.489	5.481	< 0.0001
I (sin(2 * pi * hour/24))	-1.024	0.893	-1.147	0.251571
I (cos(2 * 2 * pi * hour/24))	2.017	0.538	3.751	0.000176
I (sin(2 * 2 * pi * hour/24))	1.161	0.642	1.809	0.070488
I (cos(3 * 2 * pi * hour/24))	-1.003	0.610	-1.646	0.099846
I (sin(3 * 2 * pi * hour/24))	0.021	0.439	0.047	0.962312
I (cos(4 * 2 * pi * hour/24))	-0.608	0.357	-1.706	0.088041
I (sin(4 * 2 * pi * hour/24))	-1.159	0.369	-3.144	0.001667

Appendix 10: Parameter estimates for avian prey, based on the probability of delivery of one or more avian prey items per hour block.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-14.136	4.278	-3.305	0.000951
I (cos(2 * pi * hour/24))	16.612	6.008	2.765	0.005694
I (sin(2 * pi * hour/24))	4.085	1.906	2.144	0.032045
I (cos(2 * 2 * pi * hour/24))	-4.664	1.868	-2.497	0.012529
I (sin(2 * 2 * pi * hour/24))	-2.146	1.246	-1.722	0.085099



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