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Owls in boxes:
What prey do Ural owls (*Strix uralensis*) bring to their nestlings, when do they bring prey, and how are they handled

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Abstract

Earlier studies have investigated the feeding of owl nestlings through examining remains of animals in nests. In some species, like the Ural owls (*Strix uralensis*), this may give lacking information since they are known to remove these remains. The use of cameras may enable discovering of the subtleties in the feeding of Ural owl nestlings, more specifically the handling of different prey. I analyzed prey deliveries at 11 Ural owl nests located in Värmland county in Sweden and Hedmark county in Norway by use of video monitoring. All in all, 564 prey deliveries were registered, in which 465 of the prey were mammals, 60 were birds, 12 were frogs and 1 was a lizard. Prey deliveries were significantly lower than randomly expected from 8 hours in the morning to 17 hours in the evening and higher than expected from 18 in the evening, until 6 in the morning. Deliveries of mammals was higher than the average from 18 to 23 hours in the evening and from 3 to 6 hours in the morning. Deliveries of avian prey was higher than randomly expected from 22 hours in the evening to 3 hours in the morning. The male delivered prey directly to the female 74 times. The probability of this happening decreased as the age of nestlings increased and so did the probability of female assisting the nestlings with feeding. There are still discrepancies in this field and more similar studies should be done in other areas.

Content

Introduction

In nests, preparation of prey is often needed before delivery at the nest (Slagsvold & Sonerud 2007). For birds that swallow their prey whole the prey choice is often limited, but raptors have feet and bills designed for catching and preparing large prey enabling them to do so (Slagsvold & Sonerud 2007). The larger the prey, the more meals it will provide for the nestlings (Fosså 2013). However, larger prey takes a longer time to prepare because the raptors can only tear apart small portions (Slagsvold and Sonerud 2007; Steen et al. 2010). Such provisioning of prey is a trade-off between the time it takes for parents to forage and the benefit of removing the swallowing threshold of nestlings (Ponz et al 1999; Steen et al. 2010). Decapitating of prey prior to delivery at nest is common among owls where the parent will eat the head and make it easier for the nestling to swallow the prey. The probability of the prey to be decapitated increases with the size of the prey (Stave 2015). Birds are usually decapitated, and usually prior to delivery at the nest (Fosså 2013). Less digestible parts may also be removed (Slagsvold et al. 2010). Also, it becomes more energy-efficient to carry the prey to the nest when parts are removed (Sodhi 1992).

If the female would assist with preparing the prey for the nestlings, more food could be had because of the increase in ingestion rate, and because nestlings have problems swallowing larger prey (Fosså 2013). The ingestion rate is how much mass of prey is consumed in a certain amount of time and decreases with prey size (Sullivan 1988; Slagsvold & Sonerud 2007). The ingestion rate hypothesis states the male would be of a smaller size than the female
for them to be more adept at hunting smaller prey more profitable for smaller nestlings which the female must brood and feed (Slagsvold & Sonerud 2007). Males being smaller than females (reversed sexual size dimorphism (RSD)) is the normal pattern among raptors (Slagsvold & Sonerud 2007).

In raptors, the nestlings' need for feeding assistance from the female increases with prey mass and decrease with the age of the nestlings (Sonerud et al 2014a). A parent may often bring smaller prey rather than large ones because smaller prey would have higher profitability, which is energy containment per time of handling. Nestlings with higher age and larger body mass have a greater probability of being fed unassisted by their parent. Also, as the body mass of the prey increases, the probability of getting swallowed whole decreases and then the handling time increases (Fosså 2013).

Ural owls can be found in Scandinavia where there is not much rainfall and therefore a high fire rate (Nyhus & Mæhlen 2003). Their rate of reproduction depends much on the prey that are accessible (Lundberg 1979; Newton 1979; Korpimäki & Sulkava 1987). Prey selection of Ural owls has been extensively studied in Finland and Sweden (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987; Brommer et al. 2002a; Brommer et al. 2002b; Brommer et al. 2003; Karell et al. 2010; Lehikoinen et al. 2011).

Ural Owls are cavity-hunters and accept nest boxes (Cramp 1985; Nyhus & Mæhlen 2003). They are active during both night and day (Korpimäki & Sulkava 1987), and are K-selected predators (Korpimäki 1986) and food generalists (Lundberg 1979; Korpimäki & Sulkava 1987). Ural owls are large and display a female-biased sexual size dimorphism where the body mass of females is c. 870 g, and males c. 720 g (Mikkola 1983; Brommer et al. 2003). The female incubates and broods the nestlings, feeding them while the male hunts. When hunting, Ural owls use a sit-and-wait strategy (Cramp 1985). Ural owls prey mostly on field voles (*Microtus agrestis*), but also on water vole (*Arvicola terrestris*), bank voles (*Clethrionomys glareolus*), common shrew (Sorex araneus) and many different species of birds (Lundberg 1981; Korpimäki & Sulkava 1987; Rønning 2007). What the Ural owl parent bring and the handling of the prey is dependent on tradeoffs (Beltran & Delibes, 1994: Erkert & Kappeler 2004). The production of Ural owl nestlings increase and decrease with the abundance of field voles (Korpimäki & Sulkava 1987), and so they mostly reproduce in good vole years (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987).

Earlier studies have investigated the feeding of owl nestlings through examining remains of animals in nests. In some species, like the Ural owls, this may give lacking information since they are known to remove these remains (Korpimäki & Sulkava 1987). The use of cameras may enable discoveries of the subtleties in the feeding of Ural owl nestlings, more specifically the handling of the different prey. Rønning (2007) used video cameras placed in nest boxes to record prey deliveries, which provided new insight into how the Ural owl female feeds the nestlings and how different types of prey are handled. Generalist raptors may prove to be ideal for this kind of study because of their large variation in handling modes and handling time (Fosså 2013). Compared to many birds, nestlings of raptors have a rather long period of parental care because they need both warmth, protection, providing of food and assistance in ingesting prey and are therefore dependent on their parents (Newton 1979; Sonerud, Steen, Løw et al. 2014).

I analyzed data that have been collected from Ural owl nests in boxes with cameras. The nests were video monitored to capture food delivery to nestlings, i.e. what kind of prey the parents deliver, whether the female prepares the prey, and at what time the prey is delivered. I wanted to answer the following questions:

i) Is there any relationship between which prey the parents deliver and the time of the day they deliver them?
ii) How do the parental tasks change with the age of the nestlings?
iii) Is there a relationship between the preparation of prey and the nestlings age?

Materials and methods

Study area

The data were collected in a study area in Värmland county in Sweden (60°13´- 60°21´ N; 12°52´ - 13°16 E) with many nest boxes for Ural owl. This area is mainly boreal coniferous forest, patches of marsh- and swampland and some farmland (Nilsson 1990). Here, 9 nests and an additional 2 nests on the Norwegian side of the border, were video monitored from 9 May to 14 June 2007 by Gunnar C. Nyhus (Appendix 1). This year 21 nests were detected, which is more than the year before and the year after who had respectively 7 and 9 (Moen 2015). The trapping vole index for shrews, field vole and bank vole was at a peak in 2006 and 2007, and a low in 2005 and 2008 (G.A. Sonerud, pers. comm.)

Video observation

CCTV cameras mounted on the inside of the nest box's roof and digital video recorders were used. The digital video recorders enabled us to detect movement around the opening so we could know when the parents visited. The cameras were salmon trap cameras which detected movement. When movement was detected outside of the nest, it recorded a minute-long clip from there. These clips were timestamped. The batteries of these electronics were replaced every other day. Nest boxes were located ca. 10 m above ground. For details of the setup, see Moen (2015).

Video analysing

I examined the data by going through all the clips and marking each one that contained a delivery of a prey. What kind of prey the parent was delivering were noted. Thereafter every clip with a delivery was analyzed to discover the following (see table 1 for an example from the excel file used to analyze the data):

- The species of the prey the parents delivered was identified from tail length, head, body shape, size, eye size, and so on.

- Whether the prey was delivered from the male to the female in the box, or whether the female arrived with the prey, probably from having received it from the male outside the box.
- Whether the prey was decapitated prior to delivery or not.
- Whether the nestlings consumed the prey without assistance from the female or if the female assisted by partitioning the prey item.
- The number of nestlings and their age.

My data consisted of 563 one-minute long videos with deliveries from 11 nest boxes in the following localities: Flybäcken, Lukasmyren, Lindmyra, Fastnässätern, Fäbroslogarna, Pällslomyren, Rogberget, Svarttjärn, Öretjärn, Granberg and Hån. Of these, Lindmyra and Rogberget were in Hedmark county in Norway, and the remaining in Värmland county in Sweden. At filming, the nestlings ranged in age from 4 days to 32 days and the number of nestlings in each box ranged from 1 to 4.

Table 1: An example clip from the excel file used to analyze the data.

Locality	Nestling age	Number of nestlings	Date Time	Behavior	Prey	Delivery directly to female	Species	Decap	Feeder
Flybäcken	16	2	06.06.2007 03:05	Delivery	Bird	Yes	*Turdidae*	No	Female
Flybäcken	16	2	06.06.2007 03:58	Delivery	Mammal	Yes	*Sorex araneus*	No	Nestling

Statistical analysis

The statistical software R was used to analyze prey delivery and prey handling. First, the probability of delivery of mammals and birds as function of the time of the day. Logistic regression distribution with a yes or no response in the hour block was used, and it was corrected for nest ID.

The cosinor analysis method that was used is good when operating with a 24-hour interval. Observations were used as the number of hour blocks that was monitored and each hour block was a sample unit. The ID was a random effect to control for repeated measurements.

In addition, I tested the probability of female feeding nestlings as a function of the age of nestlings and the probability of prey being delivered directly to the female from the male owl also as function of nestling age. The probabilities were defined as the response variable and the age of nestling was the explanatory variable. The different models (M1-M3) used were decided by evaluating AICc values. M0 is the null hypothesis.

Results

Most of the deliveries, 465, were mammals. Furthermore, 60 were birds, 12 were amphibians, 1 was a reptile and 25 were unidentified. The mammals consisted mostly of bank voles, common shrew and field voles, but also a few wood lemmings (*Myopus schisticolor*) and water vole and a single least weasel (*Mustela nivalis*). Opposed to mammals, birds were consisting of a far more diverse set of species (table 2).

Table 2: Prey recorded delivered at the 11 Ural owl nests filmed

Prey	Number
Common shrew (*Sorex araneus*)	111
Bank vole (*Myodes glareolus*)	96
Field vole (*Microtus agrestis*)	79
Water vole (*Arvicola amphibious*)	6
Wood lemming (*Myopus schisticolor*)	2
Least weasel (*Mustela nivalis)*	1
Duck (*Anatidae*)	1
Common wood pigeon (*Columba palumbus*)	1
Northern wryneck (*Jynx torquilla*)	2
Anthus	2
Turdus	1
Whinchat (*Saxicola rubetra*)	1
Willow warbler (*Phylloscopus trochilus*)	9
Sylviidae	5
Willow tit (*Poecile montanus*)	3
Paridae	3
Chaffinch (*Fringilla coelebs*)	11
Fringilla	2
Eurasian siskin (*Spinus spinus*)	1
Common redpoll (*Acanthis flammea*)	1
Passerine (*Passeriformes*)	8
Lizard	1
Frogs	12
Unidentified prey	25
Total	**384**

Is there any relationship between which prey the parents deliver and the time of the day they deliver them?

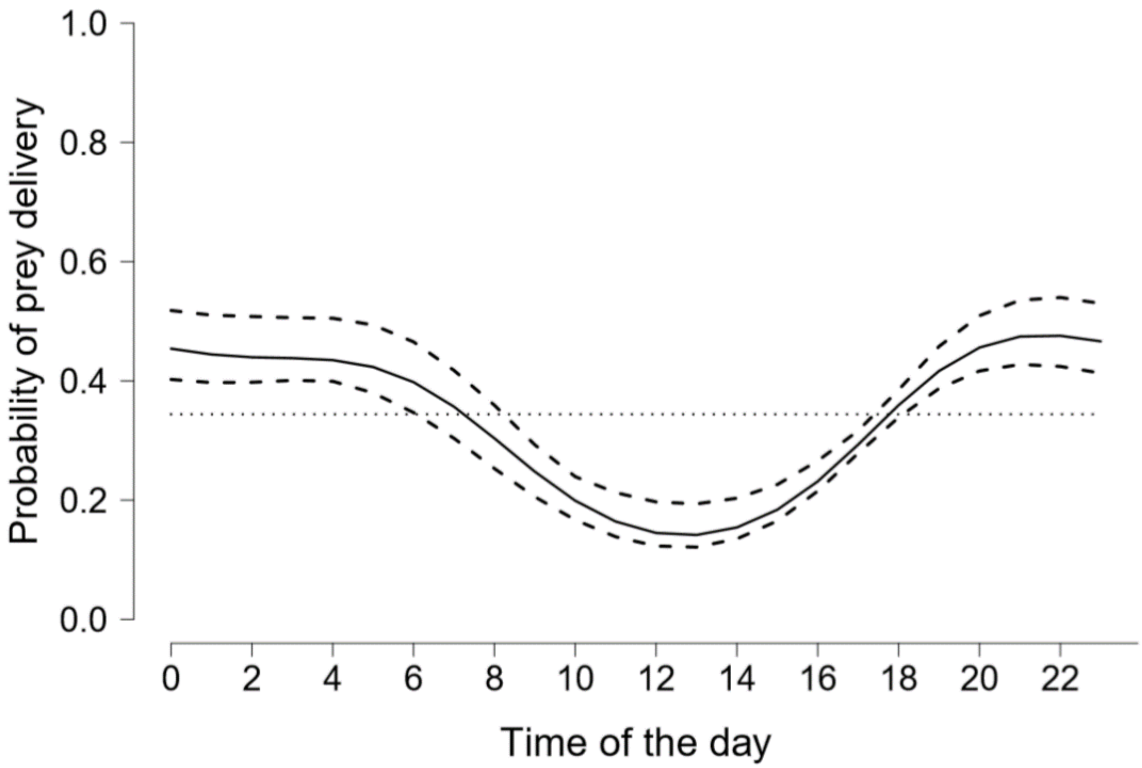

Figure 1: The probability of a prey delivery at Ural owl nests as a function of time at day and night (0-24 hours) based on appendix 3. The straight stippled line at 0.37 is the average probability of a prey delivery for 24 hours. The solid line is the prediction and the stippled lines are the confidence interval.

The probability of prey delivery was significantly higher than the average (randomly expected) from 18 hours in the evening until 6 hours in the morning, and significantly lower than the average from 8 hours in the morning until 17 hours in the evening.

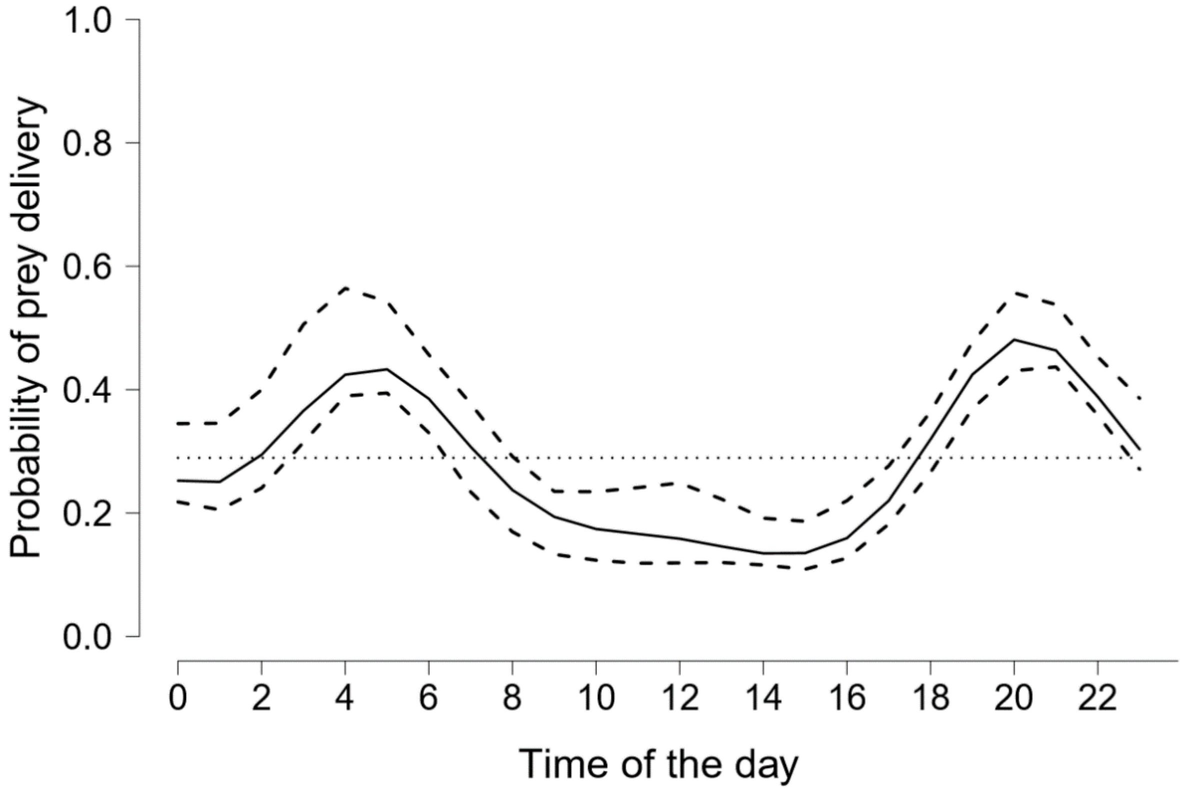

Figure 2: The probability of mammal delivery at Ural owl nests as a function of time at day and night (0-24 hours). The average probability is 0.30. See explanation for figure 1.

The probability of delivery of a mammal was significantly higher than the average from 18 hours to 23 hours in the evening and from 3 hours to 6 hours in the morning, and significantly lower than expected from 8 hours in the morning to 17 hours in the evening.

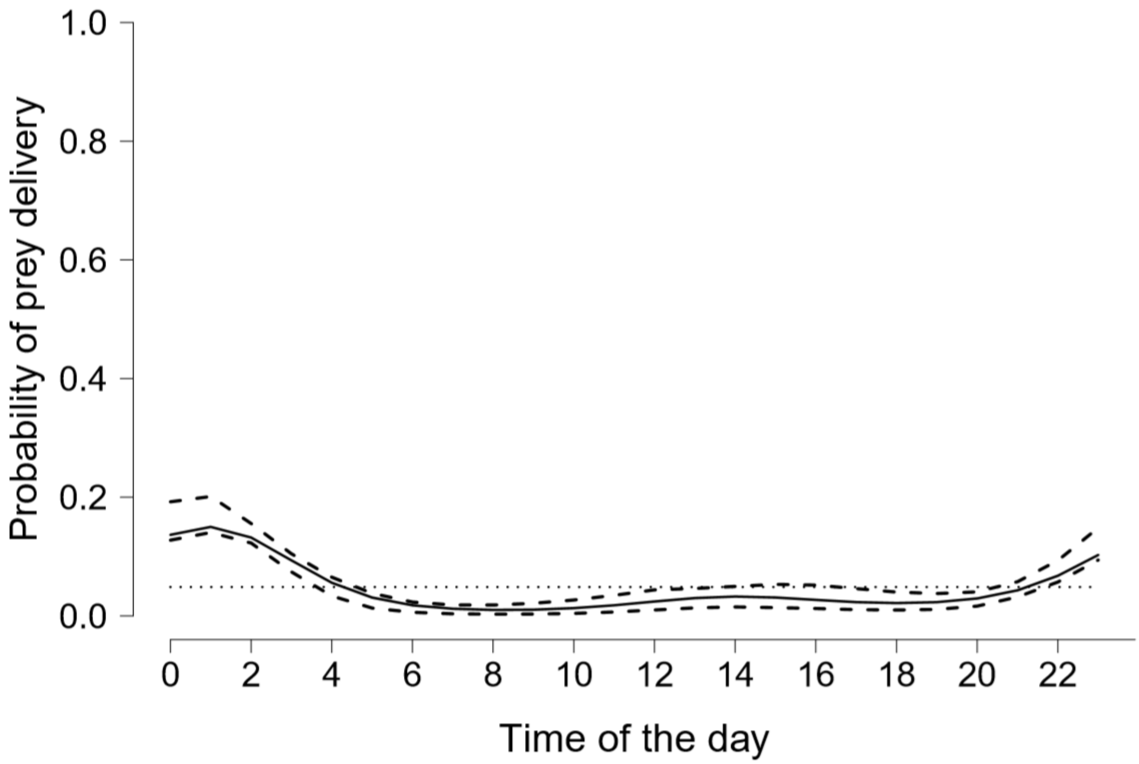

Figure 3: The probability delivery of an avian prey at Ural owl nests as a function of time at day and night (0-24 hours). The average probability is 0.05. See explanation for figure 1.

The probability of delivery of a bird was significantly higher than randomly expected from 22 hours in the evening to 3 hours in the morning and significantly lower than randomly expected from 5 hours in the morning to 21 hours in the evening, although marginally from 13 hours to 17 hours.

How do the parental tasks change with the age of the nestlings?

Table 3: Parameter estimates in the model of the probability of the male delivering prey directly to the female. Fixed effects with 563 observations and group ID of 11.

	Estimate	SE	z value	P
(Intercept)	4.0095	1.1432	3.507	<0.0001
Nestling age	-0.3317	0.0473	-7.014	<0.0001

The male delivered prey directly to the female 74 times. The probability of the male delivering prey directly to the female decreased significantly with nestling age (table 3, fig. 4).

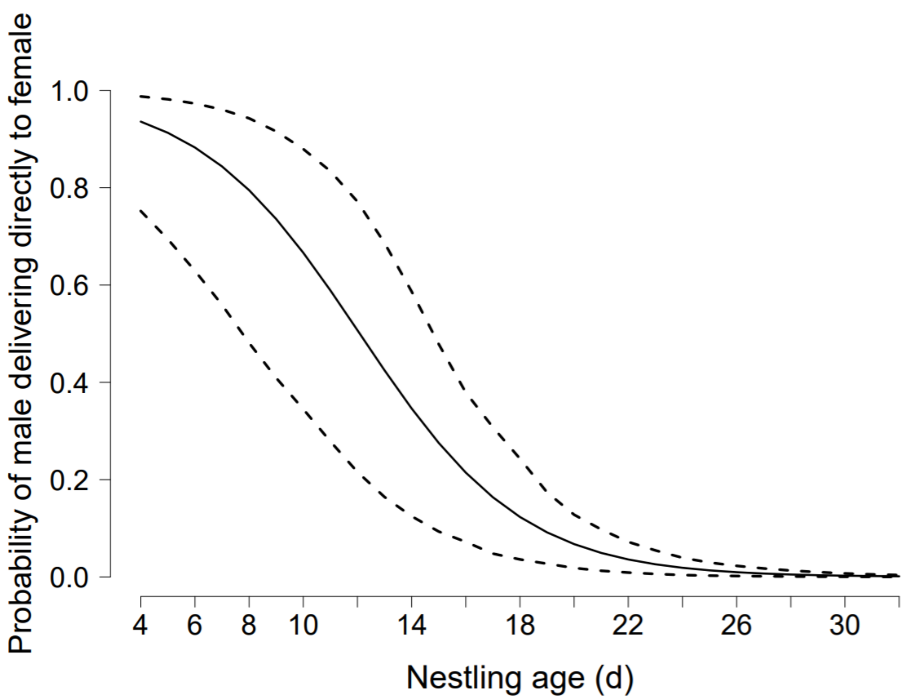

Figure 4: The probability of the male delivering prey directly to the female as a function of nestling age.

Is there a connection between the preparation of prey and the nestlings age?

Table 4: The allotment of whether the delivered prey was swallowed whole by nestlings or if they had assistance by the female in partitioning the prey.

Prey	Nestling	Female	Total
Amphibians	10	2	12
Birds	30	27	57
Mammals	355	47	402
Total	395	76	471

The female owl prepared (assisted the nestling with feeding, often by ripping small parts of the prey and feeding them to the nestlings) 76 of the prey, while 395 were swallowed whole by nestlings (table 4). Among the 60 deliveries of avian prey, 17 were confirmed being prepared by the female owl (28.3 %). In comparison, 47 of the 465 of the mammals were confirmed prepared by the female owl (10.1 %). Finally, 2 out of 12 frogs were prepared by the female (16.7 %).

Table 5: Parameter estimates in the model of the probability of assisted feeding of the nestlings by the female. Fixed effects with 481 observations and group ID of 11.

	Estimate	SE	z value	P
(Intercept)	4.32590	0.97538	4.435	<0.0001
Nestling age	-0.29721	0.04356	-6.823	<0.0001

The probability of nestling being assisted in feeding decreased significantly with nestling age (table 5, figure 6).

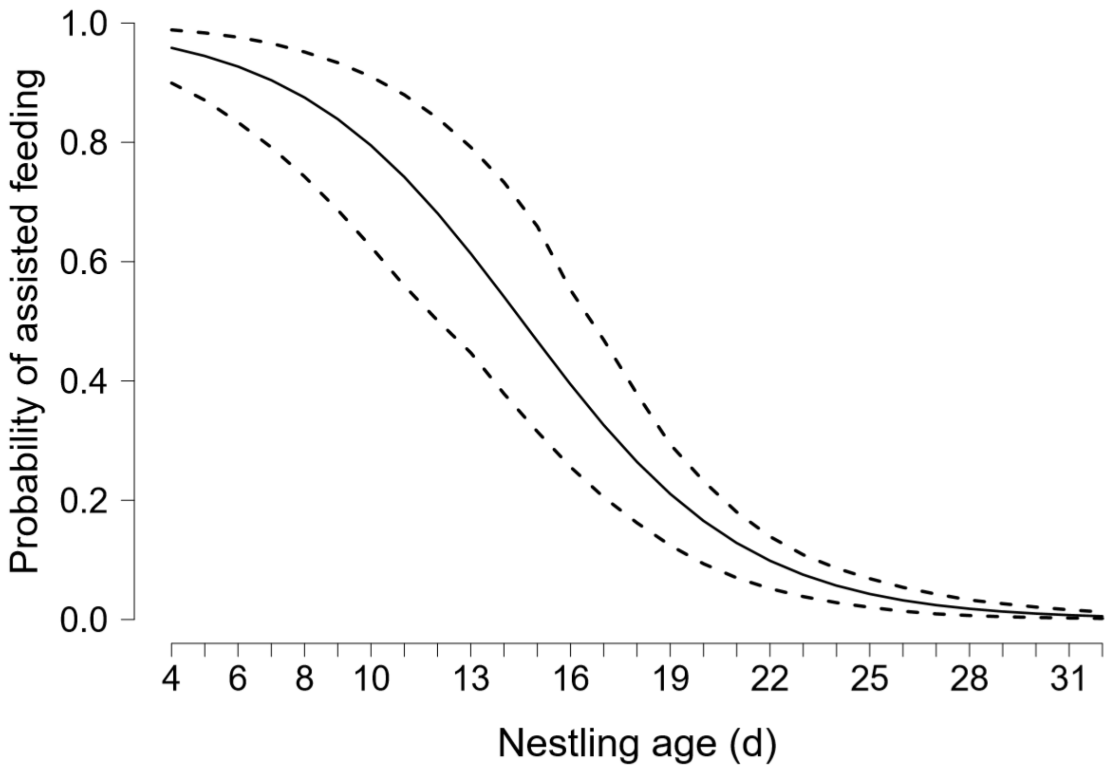

Figure 6: The probability of the female assisting the nestlings with feeding as a function of the age of the nestling.

There were 349 videos that showed prey deliveries where the heads of the prey were still attached. Most of the other prey could not be confirmed whether they had heads still attached and 5 were confirmed incidents of decapitations. No decapitation statistical analysis can therefore be done because it was impossible to confirm these unknown deliveries whether there were heads on the prey or if we simply did not see the heads.

Discussion

i) Is there any connection between what the parent delivers and the time of the day they deliver them?

Earlier studies that looked at pellets have found that Ural owls change their diet from year to year (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987). My data are from a good year for the Ural owl (Gunnar. C. Nyhus, pers.comm.). Field vole is known to be the most common prey of Ural owls (Korpimäki & Sulkava 1987, Sonerud 1992), but in my study the owls had a considerable larger array of prey species, showing their generalist nature (Lundberg 1979; Cramp 1985; Korpimäki & Sulkava 1987). I found a somewhat equal amount of bank voles and field voles, in contradiction to Rønning (2007) who found that bank voles were the most important. Since my results deviates from that of Rønning (2007) and Korpimäki & Sulkava (1987) and Sonerud (1992), Ural owls may be highly opportunistic. However, Rønning (2007) claimed his results were what they were because of a poor study area, even in peak years, forcing Ural owls to respond functionally. Korpimäki & Sulkava (1987) found that Ural owls have a functional response to bank voles. Lundberg (1981) found that in a decreasing vole year, less bank voles were eaten compared to field voles. This may all be adaptations to good and poor areas, and good and poor years. So, it may be more complex than Ural owls' reproduction increasing and decreasing with the numbers of field voles (Korpimäki & Sulkava 1987), and while the population of fully grown Ural owls is somewhat constant, the number of nestlings is not. Thus, the Ural owls reproduce to a high degree in good vole years (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987) showed by the high nestling numbers of my results.

Deliveries of avian prey increased and decreased in opposition with the increase and decrease in deliveries of small mammals. Deliveries of mammals was higher than the average from 18 to 23 hours in the evening and from 3 to 6 hours in the morning, and lower than average from 8 in the morning to 17 in the evening. In comparison, delivery of avian prey was higher from 22 in the evening to 3 in the morning and lower than average from 5 in the morning to 21 in the evening. Overall prey delivery was high most of the day, adding to that Ural owls are active during both night and day (Korpimäki & Sulkava 1987). However, they hunted mostly at night and prey delivery was lower than the average from 8 in the morning until 17 hours in the evening, supporting the view that the Ural owl is a nocturnal raptor that also hunt during twilight (Lundberg 1980a; Lundberg 1980b).

The type of prey delivered to nestlings may vary with the time of the day. Mammalian prey delivery is the highest before midnight and birds is the highest after midnight because of the diel pattern (Fosså 2013; Stave 2014). The frog delivery probability increases with lower temperatures. Hare delivery rate increases closer to midnight and such a delivery is more often followed by another hare delivery the more time that passes while the trend for birds is the opposite (Fosså 2013). Thrush (*Turdidae*) is adapted for nocturnal activity and therefore the probability of them being hunted by for example owls after midnight is high. Age of the nestlings also matter to the type of prey delivered. Shrew is delivered over other prey to younger nestlings, while delivery of other prey may increase with age. (Stave 2015)

Shrews were the most delivered prey. An important role of shrews in Ural owls' diet is being the alternative prey when there are less voles (Korpimäki & Sulkava 1987). Water voles are often more preyed on in years of less voles (Lundberg 1981). Samples of pellets also show there are many water voles involved in Ural owls' diet (Korpimäki & Sulkava 1987) and given their body mass, Jäderholm (1987) claimed them to be the most important prey. Prey delivery in my study, however, seems to indicate a wider variety of prey, more dependent on the activity of the respective prey. Both Stave (2015) and Fosså (2013) reported mammalian prey delivery to be highest before midnight and avian delivery the highest after midnight because of the diel pattern. The drop in prey delivery of small mammals around midnight may be because of the diet activity pattern of the small mammals. Also, the bird may be inactive during that time of day.

There were far less deliveries of birds than of any single mammal species of the main three, i.e. bank voles, field voles and common shrews. This contradicts Lundberg (1981) who found the opposite. My findings are more in line with Korpimäki & Sulkava (1987) who had 10 % birds among prey in nests in the Kauhava region and a 9 % for nests in the Keuruu region. As in my study, Korpimäki & Sulkava had a wide variety of bird species among prey. Jäderholm (1987) found however only 2% birds among prey by number. Rønning (2007) found deliveries of birds being 16 %. There were times when there were 12 bank vole deliveries in a row and many other lesser but similar incidents. An explanation to this could also be that the owls take advantage of when those species of prey are active.

It has been assumed that Ural owls catch birds during daytime because Ural owls are able to hunt during the day and avian prey are diurnal, even though Ural owls also are nocturnal hunters. (Korpimäki & Sulkava 1987). I found however, that Ural owls hunted for birds between sunset and sunrise, the darkest time of the day. The same was found by Rønning (2007). Birds are often roosting during night and are not on guard. Ural owl may hunt birds when they are more susceptible, thus they may be diurnally active (Korpimäki & Sulkava 1987). Nonetheless there is no doubt Ural owl can hunt birds in the dark (Lundberg 1979). In this study, avian prey was hunted at the darkest time of the day, but other prey was delivered throughout the day.

ii) Do the parental tasks change with the age of the nestlings?

Most of the prey Ural owl males deliver at the nest, are then received by the female that in turn delivers the prey to the nestlings, and the transfer from male to female often happens outside the nest (Cramp 1985). With the present data it was possible in my study to only count the number of times the male directly delivered prey to the female in the nest and compare it with the number of times the female entered the nest with a prey. The probability of the male delivering prey directly to the female decreased as the age of nestlings increased. Thus, the male entered the nest box when the nestlings were young while the female brooded the nestlings. Perhaps the male is more important in the parental care while the nestlings are young and in need of protection and warmth to a higher degree. The male seemed reluctant to deliver the prey he had caught to the nestlings when the female was unaccounted for and would often leave and return multiple times with the same prey. This fits well with the nestlings being smaller and unable to swallow larger prey whole. Larger prey takes a longer time to prepare because they can only tear apart small portions (Slagsvold and Sonerud 2007; Steen et al. 2010). Such provisioning of prey is a trade-off between the time it takes for parents to forage and the benefit of removing the swallowing threshold of nestlings (Ponz et al 1999; Steen et al. 2010).

What does not quite make sense is when the female assisted with preparing the prey for the nestlings. Why does the male bring smaller prey when the female stays at the nest and can prepare the larger prey? The male will likely not make a conscious decision of what prey to hunt but will simply take whatever he can get. However, the ingestion rate hypothesis may give us some inclination as to why the male bring smaller prey. The Ural owl male is smaller than the female, reversed sexual size dimorphism, and they are therefore more suited for hunting smaller prey (Slagsvold & Sonerud 2007). Smaller mammals may be more profitable seeing how it is causing a higher indigestion rate for the nestlings (Sullivan 1988; Slagsvold & Sonerud 2007). The Ural owls may have adapted their parental care to suit their different sizes, or the other way around. The smaller male hunts smaller prey more profitable for smaller nestlings and the female stays at the nest with the dependent nestlings while providing protection, warmth and preparing of prey (Newton 1979; Sonerud, Steen, Løw et al. 2014).

iii) Is there a relationship between the preparation of prey and the nestlings age?

A higher proportion of birds was prepared than of mammals. The average bird delivered was larger than the average mammal delivered and so the prediction that preparing of prey for nestling will increase with larger prey may have some validation. If the female were to hunt and deliver birds and larger mammals, a higher cost would also have to be payed because of the longer handling time (Sonerud et al. 2014a). On the other side if the parents were to bring more small mammals, they would have to increase the frequency of the deliveries as well, increasing the energy cost that way (Sonerud et al. 2014b). The male helping to share the cost mitigates both these problems. Fosså (2013) findings were like mine where 58 % were consumed by nestling unassisted the probability of this happening increased with the age of the nestling. However, Moen (2015) found “that unassisted prey handling by the nestlings was explained both by the body mass of the prey item and by the age of the nestling, but that the effect of the former was larger than of the latter”.

I found that the probabillity of female assisting the nestlings with feeding decreased as the age of the nestling increased. Also Sonerud et al. (2014a) found that when the age of the nestlings increased, the amount of assistance they received from the female decreased. Additionally, Sonerud et al. (2014a) found that the feeding assistance was greatly affected by the size and type of prey. The range of prey that birds choose are often limited for birds that swallow their prey whole, but raptors have feet bills designed for catching and preparing large prey enabling them to do so (Slagsvold & Sonerud 2007).

When comparing studies of Ural owls like I have done, there may be some sources of error to take into consideration, especially when comparing diets. The data from the different studies are obtained in different times and places and Korpimäki & Sulkava (1987) claims this may be cause enough for different results. Also, the methods used are different, especially through the years. For example, the collecting of pellets (Dravecký & Obuch 2009) and the use of cameras (Rønning 2007).

One source of possible error while going through data was that it was sometimes hard to see the prey or whether there was a prey delivery at all. This source of error was caused by the female owl blocking the view, since the camera was mounted in the top of the box. Further sources of error could be poor lighting and the prey being scruffy and therefore hard to identify. The nestlings would try to peck at the female bill when she arrived at the nest, even if she did not have a prey to deliver. Many deliveries in a row were consistent of many of the same species, but couldn't determine some species, only able to say they were either shrew or bank vole because of the long tail, but not being able to see the head. In one of the nests the female was shaking her head, causing the camera to start recording. Additionally, the nestlings in other nests were large and moving around quite a bit, also triggering the motion sensor of the camera. A few nestlings were seen to fledge and perched in the nest opening, maybe trying to monopolize prey that the parents brought. There is certain to be more prey during the recording than in my results, the reason being that the parent blocking the view of the camera. Humans are present in the beginning of the videos to rig them and sometimes ring the owl female. This may disturb, at least the first, data somewhat. Since the camera was activated every time it registered a movement, I observed that the female entered the nest multiple times without prey soon after humans have rigged the camera. The nest box at Granberg had particularly large nestlings and they swallowed the prey delivered so quickly that it proved difficult to identify the prey. The nest box at Hån had the opposite problem with very young nestlings who attempted to swallow whole prey by themselves, but had much trouble, causing it to take longer time than the 1 minute the camera rcorded for. Therefore, I could not see whether they managed to finish themselves or if they needed the help of the female.

Conclusion

Video monitoring of Ural owls showed they hunt a wide array of prey species. Deliveries of mammals was reduced during the darkest time of the day, but deliveries of birds increased. The male assisted the most when the nestlings were young while the female brooded them. These deliveries were mostly smaller prey, showing the adaptation of a smaller male owl to hunt smaller prey to support younger nestling in need of protection and warmth. Additionally, the nestlings were more in need of preparing of prey in the earlier stages of life. A few similar studies to mine has by now been done, but there are still discrepancies in this field and more similar studies in other areas should be performed.

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Appendix

Appendix 1: Nests filmed with the number of nestlings and their age at the time of filming.

Locality	Brood size	Nestling age (days)
Flybäcken	2	15-24
Lukasmyren	3	4-8 + 21-26
Lindmyra	3	21-24
Fastnässätern	2	18-21
Fäbroslogarna	3	24-27
Pällslomyren	1	16-20
Rogberget	4	18-20
Svarttjärn	3	25-28
Øretjärn	4	25-28
Granberg	3	29-32
Hån	2	16-18

Appendix 1: Models with AICc values.

	K	AICc	Delta AICc	AICcWt	Cum.WT	LL
Mod 3	6	413.04	0.00	0.78	0.78	-200.48
Mod 4	8	415.90	2.86	0.19	0.97	-199.88
Mod 2	4	419.79	6.74	0.03	1.00	-205.87
Mod 1	2	443.98	30.93	0.00	1.00	-219.98

Model selection based on AICc shows that M2 is chosen as the optimal for further analysis.

Appendix 2: Fixed effects from M2 from appendix 1. The cosinor method uses 1081 observations and have an ID of 11. Predicted probability of mammals and birds being delivered within an hour time block. Parameter estimates for the significant variables.

	Estimate	SE	z value	P
(Intercept)	-3.34053	0.23348	-14.308	p<0.0001

I(cos(2 * pi * Hour/24))	0.92623	0.23225	3.988	p<0.0001
I(sin(2 * pi * Hour/24))	-0.09666	0.27188	-0.356	0.7222
I(cos(2 * 2 * pi * Hour/24))	0.57097	0.22881	2.495	0.0126
I(sin(2 * 2 * pi * Hour/24))	0.48331	0.23400	2.065	0.0389

The waves I(cos(2 * pi * Hour/24)), I(cos(2 * 2 * pi * Hour/24)) and I(sin(2 * 2 * pi * Hour/24)) all have significant values they being respectively p<0.0001, 0.0126 and 0.0389.

Appendix 3: Models with AICc values.

	K	AICc	Delta AICc	AICcWt	Cum.WT	LL
Mod 4	8	1251.03	0.00	0.95	0.95	-617.45
Mod 3	6	1257.04	6.01	0.05	1.00	-622.48
Mod 2	4	1276.47	25.44	0.00	1.00	-634.22
Mod 1	2	1304.86	53.83	0.00	1.00	-650.43

Model selection based on AICc shows that M3 is chosen as the optimal for further analysis.

Appendix 4: Fixed effects from M3 from appendix 3. The cosinor method uses 1081 observations and have an ID of 11. Predicted probability of mammals being delivered within an hour time block. Parameter estimates for the significant variables.

	Estimate	SE	z value	P
(Intercept)	-0.99472	0.18984	-5.240	p<0.0001
I(cos(2 * pi * Hour/24))	0.60321	0.10629	5.675	p<0.0001
I(sin(2 * pi * Hour/24))	0.07681	0.09799	0.784	0.433104
I(cos(2 * 2 * pi * Hour/24))	-0.38314	0.10065	-3.807	0.000141
I(sin(2 * 2 * pi * Hour/24))	-0.20901	0.10253	-2.039	0.041498
I(cos(3 * 2 * pi * Hour/24))	-0.31071	0.10047	-3.093	0.001984
I(sin(3 * 2 * pi * Hour/24))	-0.06732	0.10008	-0.673	0.501202

The waves I(cos(2 * pi * Hour/24)), I(cos(2 * 2 * pi * Hour/24)), I(sin(2 * 2 * pi * Hour/24)) and I(cos(3 * 2 * pi * Hour/24)) have significant P values. They are respectively p<0.0001, 0.000141, 0.041498 and 0.001984. These signify what will be waves that differ significantly from the average.

Appendix 5: Models with AICc values.

	K	AICc	Delta AICc	AICcWt	Cum.WT	LL
Mod 4	8	1322.08	0.00	0.52	0.52	-652.97
Mod 3	6	1322.48	0.39	0,43	0,95	-655.20
Mod 2	4	1326.63	4.54	0.05	1.00	-659.30
Mod 1	2	1385.20	63.12	0.00	1.00	-690.59

M2 is decided to be optimal with the lowest AIC and fewest variables by looking at the Delta AICc. This

Appendix 6: : Fixed effects from M2 from appendix 5. The cosinor method uses 1081 observations and have an ID of 11. Predicted probability of birds being delivered within an hour time block. Parameter estimates for the significant variables.

	Estimate	SE	z value	P
(Intercept)	-0.73762	0.16935	-4.356	p<0.0001
I(cos(2 * pi * Hour/24))	0.79505	0.10237	7.766	p<0.0001
I(sin(2 * pi * Hour/24))	0.08204	0.09342	0.878	0.3798
I(cos(2 * 2 * pi * Hour/24))	-0.24165	0.09658	-2.502	0.0123
I(sin(2 * 2 * pi * Hour/24))	-0.13127	0.09606	-1.367	0.1718

The waves I(cos(2 * pi * Hour/24)) and I(cos(2 * 2 * pi * Hour/24)) have significant P values of respectively p<0.0001 and 0.0123 making them significant.