Acknowledgements

Abstract

To record prey delivery and handling, and nest of the eagle owl (*Bubo bubo*), a breeding pair was video monitored during 6 June – 25 July in Meland municipality in Hordaland County, Norway. A total of 49 prey items were recorded delivered. Of those, mammals amounted 53%, birds 36%, og amphibians 2% by frequency, while 8% were not possible to identify to any taxa. Hedgehogs (*Erinaceus europaeus)* were the most frequent prey delivered, both by frequency (39) and by biomass (68%), indicating that the pair had specialized in hunting hedgehogs. Tufted duck (*Aythya fuligula*) was the most numerous avian species, with 3 deliveries, while brown rat (*Rattus norvegicus*) was delivered twice. All prey items were delivered within 10 hours from solar midnight, defined as the darkest point throughout the night, and the majority within 3 hours from solar midnight. This strengthens the perception of the eagle owl as a nocturnal predator. Hedgehogs were to a greater extent than other prey delivered during dusk and dawn, whereas birds and rodents were delivered mainly at night. The probability that a delivered prey item was a hedgehog decreased as precipitation increased. The probability that a delivered prey item was a bird increased as nestling age increased. The probability that a delivered prey item was a duck increased as deviation from solar midnight increased. The probability that the eagle owl delivered an item of the same prey type as the previous one delivered increased with increasing deviation from solar midnight. The probability that the eagle owl delivered an item of the same species as the previous one delivered decreased as the time since previous delivery increased. Birds were the only prey that was decapitated prior to delivery, and 73% of avian prey was delivered decapitated. The probability of a bird being decapitated prior to delivery increased as its body mass increased. The probability that the nestlings fed unassisted increased as their age increased, and decreased as prey mass increased. As more traditional diet analyses based on pellets and prey remains has proved to be biased, video monitoring proves to be a useful tool when mapping diet and breeding biology in raptors. This in turn can be implemented in the preserving of birds of prey, because identification of their food sources is essential from conservation considerations. However, only two eagle owl nests has previously been video monitored for this purpose, thus a currently small basis of data makes conclusions daring for now.

Sammendrag

For å undersøke byttedyrsseleksjon og byttedyrshåndtering ble et hekkende par hubro (*Bubo bubo*) videofilmet 6 juni – 25 juli i Meland kommune i Hordaland. Totalt ble det levert 49 byttedyr på reiret. Av disse utgjorde pattedyr 53%, fugl 36%, og amfibier 2%. 8.2% av leverte byttedyr lot seg ikke identifisere til noe taksonomisk nivå. Piggsvin (*Erinaceus europaeus)* var det hyppigst leverte byttedyret både av frekvens (39%) og i biomasse (68%). Uten sammeligning var piggsvinet det viktigste pattedyret, og det er naturlig å anta at paret hadde spesialisert seg i jakt på piggsvin. Toppand (*Aythya fuligula*), levert 3 ganger var den mest hyppige arten av fugl levert på reiret, mens brunrotte (*Rattus norvegicus*) ble levert 2 ganger. Alle byttedyr ble levert innen et tidsom på 10 timer fra solar midnatt, definert som døgnets mørkeste tidspunkt, majoriteten av disse innen 3 timer. Dette styrker oppfatningen av hubro som et nattaktivt rovdyr. Piggsvin ble i større grad enn andre byttedyr levert i skumringen, mens fugl og gnagere i hovedsak ble levert om natten. Sannsynligheten for at et levert byttedyr var et pinnsvin minket med økende nedbør. Sannsynligheten for at et levert byttedyr var en fugl steg ettersom ungenes alder økte. Sannsynligheten for at et levert byttedyr var en and økte med økt avstand fra solar midnatt. Videre økte sannsynligheten for at et levert byttedyr var av samme dyreklasse som forrige leverte bytte med økt avstand fra solar midnatt, mens sannsynligheten for at samme art ble levert minket ettersom tiden siden forrige levering økte. Fugler var den eneste dyreklassen som var dekapitert før levering, og 73% av leverte fugler var dekapitert. Sannsynligheten for at en fugl var dekapitert før levering økte ettersom vekten hos fuglen økte. Sannsynligheten for at ungene spiste uassistert av byttedyrene økte ettersom de ble eldre men minket ettesom størrelsen på byttedyret økte.

Mer tradisjonelle diettanalyser, f.eks gulpebolleanalyser, har vist seg å kunne være feilaktig og er høyst avhengig av kvaliteten hos observatører. Derimot har videoovervåkning vist seg som et godt verktøy for nøye kartlegging av rovfuglers diett og atferd. I sin tur kan dette implimenteres i forvaltningen av artene, ettersom identifisering av fuglenes byttedyr er essensielt i bevaringshensyn. For hubro er dette gjort bare to ganger tidligere, og følgelig bør resultatene foreløbig behandles med forsiktighet.

Table of contents

Introduction

Unlike most birds, raptors does not capture food with their beak and swallow their prey whole. Instead they capture prey with their feet, and use their beak to slice killed prey into manageable parts. This allows them to feed on prey of relative large size, as their swallowing capacity has a lesser influence on prey selection (Slagsvold et al. 2010). Given this large prey-size and small morsels swallowed in turn while eating, raptor meals are a time consuming effort (Slagsvold & Sonerud 2007; Slagsvold et al. 2010; Steen et al. 2010).

The majority of raptors have asymmetric parental roles, where the male hunt whilst the female is tied to the nest for incubation, brooding and preparing of food to nestlings (Sonerud et al. 2014). Due to poor technique, small beaks and low swallowing capacity, nestlings are namely fed with morsels from dismembered prey, because whole prey is unmanageable for nestlings, for a period of time. This preparing of food for dependent offspring among raptors is considered a trade-off between benefits for the nestling and costs for the parents as time spent on self foraging is reduced (Steen et al. 2010). A study conducted by Steen et al. (2012) also suggest that the food demand of broods might increase with age, making the time constraints set by self-feeding and provisioning for nestlings even tighter. This could explain why some prey items have non-essential body parts removed prior to delivery at the nest, for instance by decapitation, as this allows the female to spend more time on feeding herself and broods and less on provisioning (Rands et al. 2000). How soon the nestlings become able to handle prey unassisted, determines for how long the female is confined to the nest as sedentary processor of the prey provided by the male (Sonerud et al. 2014). The feeding constraint hypothesis (Slagsvold & Wiebe 2007; Steen et al. 2010) suggest that prey brought to the nest should be of decreasing body mass as the nestlings get older, and hence expected to feed unassisted, because prey of lower body mass is believed to be more manageable for nestlings. In turn this would mitigate the cost of having offspring, allowing the female to spend more time on self-foraging, as her time confined to the nest would be minimized.

One measure of efficiency among foraging raptors is their ingestion rate, e.g. prey mass consumed per unit of time. This rate is found to drop with increasing prey size (Slagsvold & Sonerud 2007), presumably caused by the thicker skin and skull of larger prey which lengthens the handling time. These findings further suggest an explanation of the reversed sexual size dimorphism (RSD) in raptors, as the hunting male will target smaller prey related

to its own size, thus increasing the ingestion rate, whilst the female tends to the nest (Sonerud et al. 2014). Consequently, this is believed to favour a sexual selection towards smaller males. This evolutionary approach on RSD, launched by Slagsvold & Sonerud (2007), is entitled the ingestion rate hypothesis.

The eagle owl (*Bubo bubo)* occurs in the western Palearctic (Cramp 1985), and is the largest owl in the world. Plumage does not differ between sexes but the female is markedly larger than the male, respectively weighing 2,2–4,2 and 1,8-2,8 kg, wings spanning 150 – 180 cm (Hagen 1952). In Norway concerns has been raised regarding the species declining numbers for the past 100 years. In 2010 the eagle owl was categorized as endangered in The 2010 Norwegian Red List for Species (Kålås et al. 2010). From a national mapping project carried out between 2008-2012, it was estimated that the Norwegian population counted 451-681 breeding pairs (Øien et al. 2014).

The eagle owl is a suitable object of research in studies of prey-handling strategies in raptors for numerous reasons: i) It has a broad diet consisting of mammals and birds in a variety of sizes, amphibians, and even insects (Alivizatos et al. 2005). ii) It is a central place forager during nesting, meaning that meals are consumed at the same location throughout the breeding period, making it suitable for a study based on stationary cameras. iii) As the size of prey is relatively large, only one prey item can be carried to the nest at a time, making it a single prey loading central place forager as explained by Sonerud (1985). Such a strategy is ideal for analyses of prey items and handling because items can be considered one by one.

The female performs all incubation and brooding (Cramp 1985), whilst the male hunt and provides both the female and the young with prey. Prey items are relatively large and often unmanageable for the young without maternal assistance, therefore the female prepares and feeds the young with the prey provided by the male (Cramp 1985; Fosså 2013). The nest is located on the ground, preferably in open landscape (Cramp 1985). In Spain, the number of fledged young have been found to be positively related to the amount of open landscape surrounding the nest (Penteriani et al. 2002).The eagle owl is nocturnal, hunting mainly at night, and most prey have been found to be delivered at nest between 22 hours and 04 hours (Mysterud & Dunker 1983; Cramp 1985; Penteriani, V et al. 2007; Fosså 2013).

In previous studies, data on prey deliveries in raptor nests have mainly been gathered by direct observations from a hide or by analyses of pellets and prey remains. Such data may be biased due to uncertainty in determining prey species from direct observations and because the amount of remains would depend on type and size of prey (Slagsvold et al. 2010). A more precise estimate can be gathered by mounting cameras at the nest site, consequently filming delivery and handling of prey. More recent studies, applying such a method, have proven excellent for determining food habits of raptors (Steen 2009; Slagsvold et al. 2010; Steen 2010; Fosså 2013; Sonerud et al. 2014; Nielsen et al. 2015). However, only two nests of breeding eagle owls has been filmed for this purpose (Fosså 2013; Nielsen et al. 2015), making the data basis scarce.

Here I analyse prey handling and composition of prey in an eagle owl nest during nesting. A key element was to identify what factors affected choice of prey and prey size, because this is central in the feeding constraint hypothesis and is believed to cause sexual size dimorphism in raptors. Because our knowledge of prey handling and behaviour in breeding pairs of eagle owl is yet based on few sources of data, this study will help understand the true quantity of food delivered at nests, and increase our understanding of how eagle owls best raise viable offspring. Additionally, surveying food habits of raptors are essential for conservation purposes because diet is believed to strongly influence survival and breeding success (Penteriani et al. 2002; LourenÇo & Sergio 2006). Knowledge regarding the preferred food of eagle owl can contribute to wiser decision-making in relation to land use and hunting restrictions among others. The eagle owl´s scarce population in Norway further emphasizes the importance of such knowledge.

Methods

Study area

This study is based upon fieldwork in conducted June – July 2015 in Meland (Figure 1); a coastal island municipality located in Hordaland county in south-western Norway (60°57N´; 5°07´E). The area is situated in the southern boreal region (Bjerkely 2008). Coastal rocks characterize the outer part of the region, facing the coast and straits. Hilly terrain is prominent, alongside exposed mountain outcrops. Between these bare mountains small lakes and creeks are found. Mosaics of open heath, coastal heath, small scrub and marsh are common, while in sheltered depressions woodland may occur. The more hardy Sitka spruce *(Picea sitchensis)* however, rises loftier. Inner parts of the region include denser cover of deciduous, coniferous and mixed forest (Puschmann 2004). In several parts of the region cultivated land and pastures are present, many intensively managed and fertilized (Hegland 2002). Close to the monitored nest, several cabins, farms, and resident settlements are present. This provided the micro-area with an anthropogenic character as associated trails and roads ran trough parts of the landscape, and as grazing livestock were common. Also, the study nest was located ca. 2 km from a highly productive wetland area. In 1985 the wetland area was given state protection especially in consideration of a rich and varied birdlife.

Figure 1. Study area

Monitoring the eagle owl

Delivery of prey, and prey handling, was recorded using two miniature surveillance CCD (charged coupled device) cameras mounted at the nest. Two nestlings inhabited the nest, which was located on the ground, underneath a large rock ledge. The reason for applying two cameras, and not one, were due to walking-excursions carried out by the nestlings. Such excursions, usually starting when the nestlings are 2-4 weeks old (Cramp 1985), may exceed the area covered by one camera. Therefore, two separate cameras, covering a relative large area between them, were applied to provide sufficient data collection. One was installed near ground level to capture detailed images of prey and prey handling, while the other was

installed ca. 1.5 m above ground level to provide an overview of the nest. A similar placement of cameras was used by Fosså (2013).

Both cameras were motion-triggered, thus a new recording started whenever a movement sufficient enough to trigger the cameras sensitivity level occurred. The motion detection sensitivity was set to 5 (min 0, max 9). When movement ceased, recording stopped. Both cameras were fitted with infrared lights to enable recording of nocturnal activity.
A 100 m long BNC video and power cable linked each camera to its own DVR recording device (Mini Security Recorder). To obtain accurate timing of nest activity, time and date were set on the device before installation in field. The recordings were stored file by file on 32 GB SD-cards, before being transferred to a laptop computer and finally to two separate external hard drives. The SD-cards were replaced on average every four days.
Two 12 V batteries (80 Ah) located beside the DVR supplied both recording devices and cameras with power. The recording devices were stored in a waterproof container that, along with the batteries, were placed under a tarpaulin in order to keep it dry. This method is a variant of that described by Steen (2009).

Analysing recorded material

During the 50 days (gross 1 200 h, net 1 039 h) of monitoring during 6 June – 25 July, a total of 42 567 video files were obtained and stored for detailed review. The majority of the recorded files were triggered by moving vegetation or roaming nestlings, rather than delivery and handling of prey, and were thus excluded from subsequent analysis. Therefore, only 1 014 files, containing relevant events, were kept for further analyses. For reasons unknown the camera equipment failed to record from 4 July (14:47) to 7 July (21:20), thus these dates are missing.

Applying a 55-inch monitor, and rerunning recordings of prey deliveries repeatedly until a frame favourable for identification of prey appeared, facilitated the prey identification process. Prey items were placed within one of three main prey categories: mammal, bird or amphibian. Thereafter, each item was identified to the lowest taxonomic level possible, the majority was identified to species.

Subsequently, several response and explanatory variables associated with each prey delivery were scored during the screening: Time and date were scored in order to map the daily hunting activity, to calculate the time elapsed between each prey delivery, to measure deviation from solar midnight and whether the delivery was before or after solar midnight. The age of nestlings was estimated to survey how quantities of prey and prey body mass changed as the young grew older, if the diet changed, and how prey handling changed with nestling age. Prey body mass (g) was estimated to see if it affected whether the nestlings ingested the meals themselves, rather than having the female parent feed it to them. Therefore, whether the nestlings ate unassisted or not was also scored. The stochastic variables precipitation (mm) and ambient temperature (°C) in the study area was scored to see if it affected choice of prey, and subsequent prey handling. The sex of delivering parent was scored to examine if there were sex roles in the upbringing of offspring. Thereafter, I scored whether or not the prey was decapitated prior to delivery to see if different prey types required different handling outside the nest, and whether or not it was affected by time of the day or the age of the nestlings. Finally, if a delivered prey were of the same prey species, or prey group as the previous one delivered, was scored separately to see if the eagle owl were consistent in prey selection for successive hunts.

Measuring variables

Time (hour/minute/second) and date (D/M/Y) were set on the recording device before the monitoring was started. It ran continuously, appearing in the bottom right of the frame (see Appendix 1), and was scored at each delivery as a parent landed at the nest with a prey item.

By comparing my video material with photos in Penteriani et al. (2005) the nestlings were estimated to be 34 days old at the date of mounting the camera 6 June. This estimate was validated through mail correspondence with V. Penteriani (pers. comm.)

Prey body mass for avian species was taken from literature. Bird body mass has a relatively small intraspecific variation; therefore a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp & Simmons 1977; Cramp & Simmons 1983; Cramp 1988; Cramp & Perrins 1994; Selås 2001). Hedgehogs *(Erinaceus europaeus)* delivered were compared to each other to obtain relative body mass in order to make an estimate for each individual, as recommended by Fosså (2013) for hares *(Lepus*

timidus). The comparisons was made using transparent paper that was laid on top of the monitor, enabling the outline of each hedgehog to be sketched before compared to each other. Body mass of rodents was taken from data on trapped specimen (G.A. Sonerud, pers. comm.). Prey body mass for all prey is set as gross body mass, i.e. the weight of the prey before potential decapitation or other dismembering of body parts.

Data on precipitation and ambient temperature in the study area were obtained from Florida weather station located in Bergen municipality, Hordaland County (60°38,30N´; 5°33,27´E), which was the nearest weather station, located 28.9 km from the study area. The data is registered by The Norwegian Meteorological Institute and is available from eklima.met.no. Temperature was logged once every hour, and precipitation once every 12 hours, and is entered in degrees of Celsius and mm, respectively. Regarding precipitation, prey deliveries were scored as the registration closest in time.

Solar midnight, which is defined as the darkest time of the day, was set at 01.42 hours (NOAA). Because solar midnight is dependent on the time of year it was set as an average for the monitoring period, which was 1 July.

When calculating the time between each delivery, the delivery occurring first after missing dates was excluded. Prey deliveries occurring after unidentified prey species were not scored to whether the eagle owl selected the same prey species on successive hunts. Whether the eagle owl was consistent regarding prey types for successive hunts was scored in the same manner.

Statistical analysis

The majority of statistical modelling and accompanying models was designed using the statistical software JMP ® (SAS Institute Inc. 2015) version 12.1.0. Logistic regression models were made for each dependent variable to reveal which explanatory variables that were affecting. Because the combination of explanatory variables could be relative large, they were included in a full model and successively removed until only significant ($p<0.05$) or marginally non-significant ($0.05<p<0.10$) variables remained in the model. The models included are hence the best explanatory models identified by stepwise backwards elimination

based on log ratio tests. The inclusion of marginally non-significant effects was due to a relatively small dataset. Parameter estimates are tested with Wald tests.

To reveal circadian activity rhythm and different delivery patterns of different prey among different hours of the day, the statistical software R ® version 2.10.0 (The R Foundation for Statistical Computing) was applied. The models were based on mixed-effects multi-periodic logistic regression models (Pinheiro & Bates 2000), as explained by Pita et al. (2011). To estimate the probability of a prey being delivered within an hour-block, the response variable for each hour-block was whether or not at least one prey item was delivered. The analysis was started by scoring whether a delivery occurred or not, denoted by "yes" or "no", to each of the current hour-blocks throughout the whole monitoring period; hence the observation number was the number of hour blocks observed. This was done both for prey in general and for the prey of highest delivery frequency (see Appendix 2,3,4,5).

Ethical note

Several measures were implemented out of consideration for the eagle owl`s behaviour and avoidance of human activity. The eagle owl is extremely sensitive to disturbance, and has been found to abandon eggs or even nestlings when disturbed (Cramp 1985). To prevent such interference during early nesting, the equipment was not installed until 6 June, when the nestlings were already 34 days old. Also, the video and power cable was 100 m long, so that I was able to operate recording devices and batteries without getting close to the nest. I did not approach the nest, except when mounting or demounting cameras. The mounting required roughly 30 minutes, and normal parental and nestling behaviour was resumed shortly afterwards. The brood was not abandoned during this study, and both nestling reached fledging age.

Results

Prey delivered

During 1 039 hours of monitoring, a total of 49 prey items were delivered at the nest. Thus, the prey delivery rate was 0.047 prey items per hour, i.e. 1.12 per day. Due to poor video quality or prey deliveries taking place beyond camera range, 4 prey items could not be identified to prey group or species. Thus, 45 prey items formed the basis for analyses. An additional 2 prey items could not be identified at species level (Table 1). Consequently, these items were scored to prey group but classified as unidentified in regard to species.

The most frequent prey type delivered were mammals (53.1%), followed by birds (36.7%) and amphibians (2.0%) (Table 1). These accounted for 73.0%, 26.9% and 0.1% of the total biomass delivered, respectively (Table 2). The most common prey species delivered at the nest was the hedgehog, accounting for 38.8% of all delivered prey items, and 68.4% of total biomass delivered. No other prey species was as important. Hedgehogs were the only prey where remains were frequently removed from the nest after feeding sessions. The most common bird species delivered was the tufted duck (*Aythya fuligula*), accounting for 6.1% of all delivered items, and 4.7% of total biomass. Thrushes (*Turdidae*), other passerines (*Passeriformes*) and small rodents (*Rodentia*) which could not be identified to species level, made up an equal quantity as the tufted duck. However, these contributed only 1.9%, 0.3% and 0.6% of total biomass, respectively (Table 2). In contrast, Eurasian curlew (*Numenius arquata*) and hooded crow (*Corvus corone*) was delivered only once, but comprised 4.4% and 3.2% of total biomass (Table 2). Unidentified species of the duck family (Anatidae) were delivered twice, and contributed 4.1% of total biomass. Average ± SE gross body mass for all prey was 351.1 ± 40.4 g (n = 45). For mammals and birds average ± SE gross body mass was 443.1 ± 49.4 g (n = 26), and 236.7 ± 59.4 g (n = 18), respectively. The difference in average body weight of mammals and birds was significant (variance; F = 7.13, p = 0.011).

Among all prey items delivered, 8.2% could not be identified at group level, while a further 4.0% were not identified at species level. These are not included in Table 2.

Table 1. Prey items delivered at the eagle owl nest during the period of video monitoring, assigned to prey category, with number (N) and frequency (%).

Prey category	Number (N)	Frequency (%)
Black- headed gull (*Chroicocephalus ridibundus*)	1	2.0
Tufted duck (*Aythya fuligula*)	3	6.1
Hooded crow (*Corvus corone*)	1	2.0
Eurasian woodcock (*Scolopax rusticola*)	1	2.0
Eurasian curlew (*Numenius arquata*)	1	2.0
Eurasian siskin (*Carduelis spinus*)	1	2.0
Northern lapwing (*Vanellus vanellus*)	1	2.0
Trush sp. (*Turdidae*)	3	6.1
Passerine sp. (*Passeriformes*)	3	6.1
Duck sp. (*Anatidae*)	2	4.1
Unidentified bird	1	2.0
Bird total	18	36.7
Hedgehog (*Erinaceus europaeus*)	19	38.8
Brown rat (*Rattus norvegicus*)	2	4.1
Wood mouse (*Apodemus sylvaticus*)	1	2.0
Rodent sp. (*Rodentia*)	3	6.1
Unidentified mammal	1	2.0
Mammal total	26	53.1
Common frog (*Rana temporaria*)	1	2.0
Amphibian total	1	2.0
Unidentified	4	8.2
Total	49	100.0

Table 2. Prey items delivered at the eagle owl nest during period of monitoring, assigned to prey category, with estimated body mass per unit of prey species (g), total biomass per prey species (g), and percentage of total biomass (%).

Prey category	Body mass (g)	Biomass (g)	Biomass (%)
Black- headed gull	300	300	1.9
Tufted duck	[1]250	750	4.7
Hooded crow	500	500	3.2
Eurasian woodcock	300	300	1.9
Eurasian curlew	700	700	4.4
Eurasian siskin	10	10	0.1
Northern lapwing	200	200	1.3
Thrush sp.	100	300	1.9
Passerine sp.	[2]16	50	0.3
Duck sp.	[3]325	650	4.1
Unidentified bird	500	500	3.2
Bird total		4 260	26.9
Hedgehog	[4]570	10 830	68.4
Brown rat	250	500	3.2
Wood mouse	25	25	0.2
Rodent sp.	31	95	0.6
Unidentified mammal	100	100	0.6
Mammal total		11 550	73.0
Common frog	20	20	0.1
Amphibian total		20	0.1
Unidentified			
Total		15 830	100.0

[1] Duckling
[2] Mean estimate (range 15 - 20)
[3] Mean estimate (range 250 – 400)
[4] Mean estimate (range 250 – 900)

Hunting activity

Whether delivered before or after solar midnight, all prey items were delivered within 10 hours from solar midnight, the majority within 3 hours from solar midnight (Figure 2). The mean ± SE deviation from solar midnight was 2 h 31 min ± 40 min, and the median deviation was 1 h 18 min. The hour blocks of highest delivery frequency was 24.00–01.00, 01.00-02.00 and 03.00-04.00 who had a 22.7, 11.3, 18.6% probability of prey delivery, respectively, taken from the monitoring period as a whole (Figure 3). Different prey types showed different temporal distribution with regard to delivery at the nest. Hedgehogs were to a greater extent delivered during dusk and dawn than were rodents and birds, which more often were delivered during the darkest hours of the night (Figure 4).
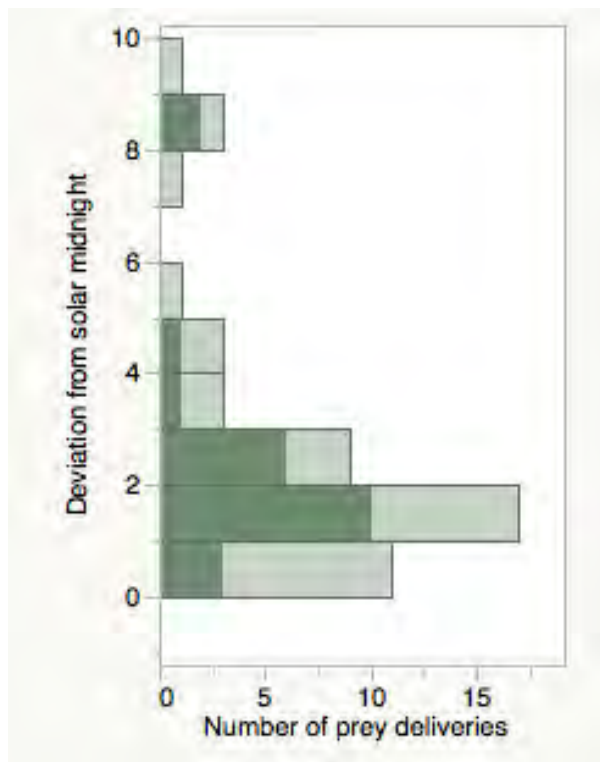
Figure 2. Temporal distribution of prey deliveries at the eagle owl nest, expressed as deviation from solar midnight. Dark areas within the bars marks deliveries made after solar midnight (morning), while lighter areas marks deliveries made before solar midnight (evening).
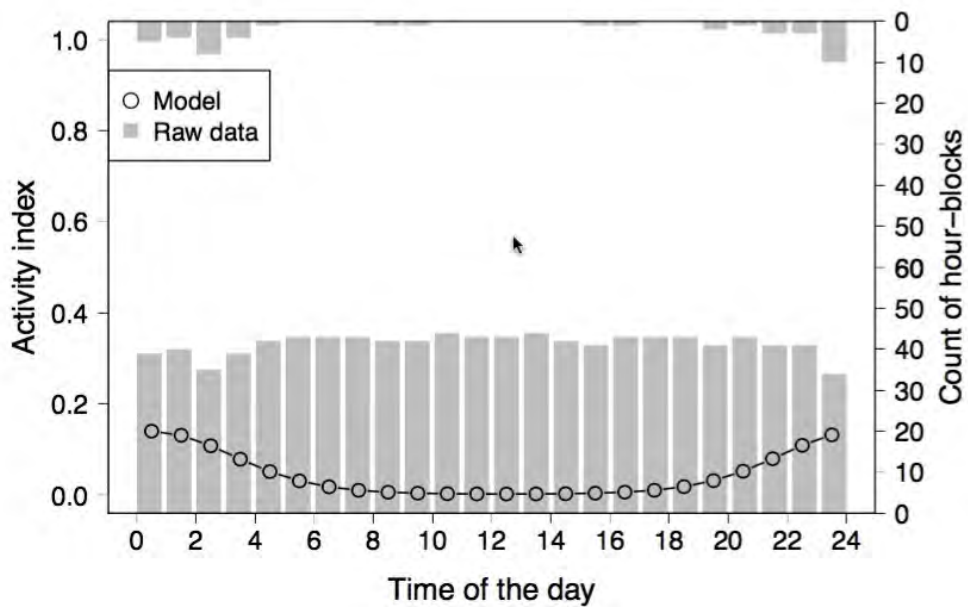
Figure 3. Temporal distribution of prey items delivered at the eagle owl nest. The activity index (circles, left scale) denotes the probability of at least one prey item being delivered within a given hour-block, while the observation frequency (lower bars, right scale) denotes the total amount of hours observed (N = 1 039), and prey deliveries (upper bars, upper right scale) denotes the actual number of prey deliveries.

Figure 4. Temporal patterns of delivery of main prey types (hedgehog, birds and rodents), at the eagle owl nest. The red vertical line indicates sunset (23:08:28), the black vertical line indicates solar midnight (01:42:24) while the green vertical line indicates sunrise (04:16:29), all given for the average date during the monitoring period (1 July).

Prey selection

To reveal the factors that affected the probability that the prey item delivered was a hedgehog rather than another prey, the following six explanatory variables were included in a full model and successively removed until only significant (p<0.05) or marginally non-significant (0.05<p<0.10) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, ambient temperature, precipitation and nestling age. Of these, precipitation and nestling age was retained in the final model as marginally non-significant factors (Table 3). The probability that a delivered prey item was a hedgehog, rather than another prey type, decreased with increasing precipitation during the day of delivery (Figure 5).

Table 3. Logistic regression model of the probability that a prey item delivered at the eagle owl nest was a hedgehog, rather than another prey type. Whole model: N = 44, x^2 = 7.09, df = 2, p = 0.028.

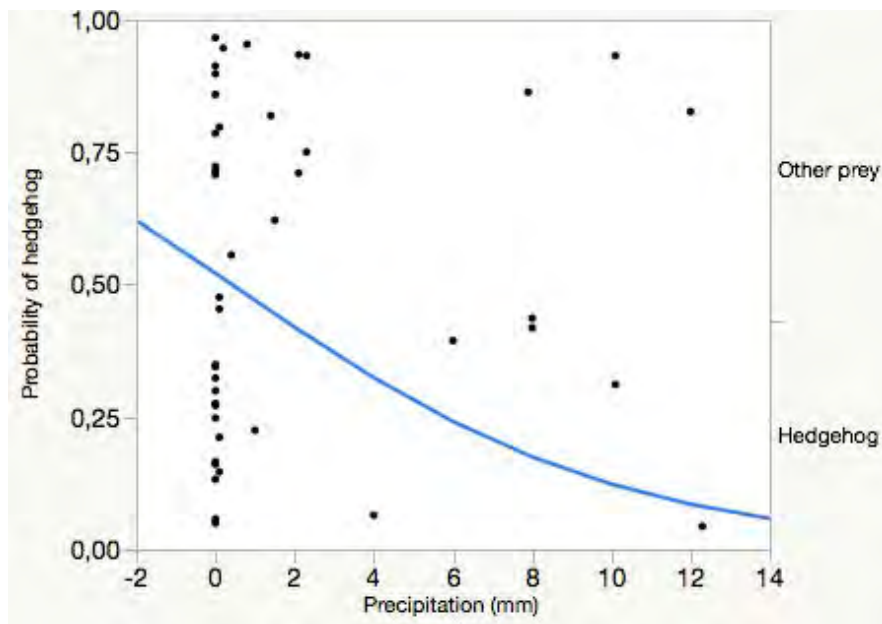| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	2.199	1.316		2.79	0.094
Precipitation (mm)	-0.214	0.111	1	3.65	0.056
Nestling age	-0.038	0.023	1	2.78	0.095

Figure 5. The probability that a prey item delivered at the eagle owl nest was a hedgehog rather than another prey type, as a function of precipitation. Whole model: N = 44, x^2 = 4.09, df = 1, p = 0.043.

To disclose the factors that affected the probability that the prey item delivered was a bird rather than another prey, the following six explanatory variables were included in a full model and successively removed until only significant (p<0.05) or marginally non-significant (0.05<p<0.10) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, ambient temperature, precipitation and nestling age. Of these, nestling age was retained in the final model as a marginally non-significant factors (Table 4). The probability that a delivered prey item was a bird, rather than another prey type, increased with increasing nestling age (Figure 6).

Table 4. Logistic regression model of the probability that a prey item delivered at the eagle owl nest was a bird. Whole model N = 44, x^2 = 3.37, df = 1, p = 0.066.

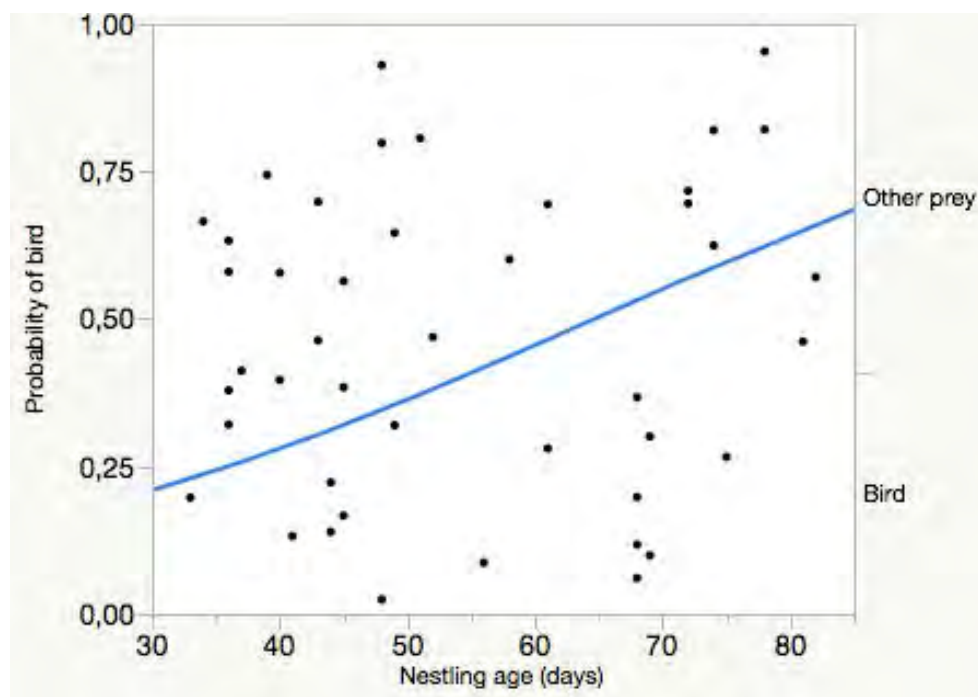| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	-2.477	1.234		4.02	0.044
Nestling age	0.0383	0.021	1	3.19	0.074

Figure 6. The probability that a prey item delivered at the eagle owl nest was a bird rather than another prey type, as a function of nestling age. Whole model: N = 44, x^2 = 3.37, df = 1, p = 0.066.

Because bird and hedgehog were the most frequently delivered prey types six explanatory variables were included in a full model to reveal which affected the probability that the prey item delivered was a bird rather than a hedgehog: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction of the former two, ambient temperature, precipitation and nestling age. These were successively removed until only significant (p<0.05) or marginally non-significant (0.05<p<0.10) effects remained in the model. Nestling age and precipitation were retained in the final model as marginally non-significant factors (Table 5). The probability that a delivered prey item was a bird, rather than a hedgehog, increased with increasing nestling age (Figure 7).

Table 5. Logistic regression model of the probability that a prey item delivered at the eagle owl nest was a bird, rather than a hedgehog. Whole model N = 37, x^2 = 8.39, df = 3, p = 0.038.

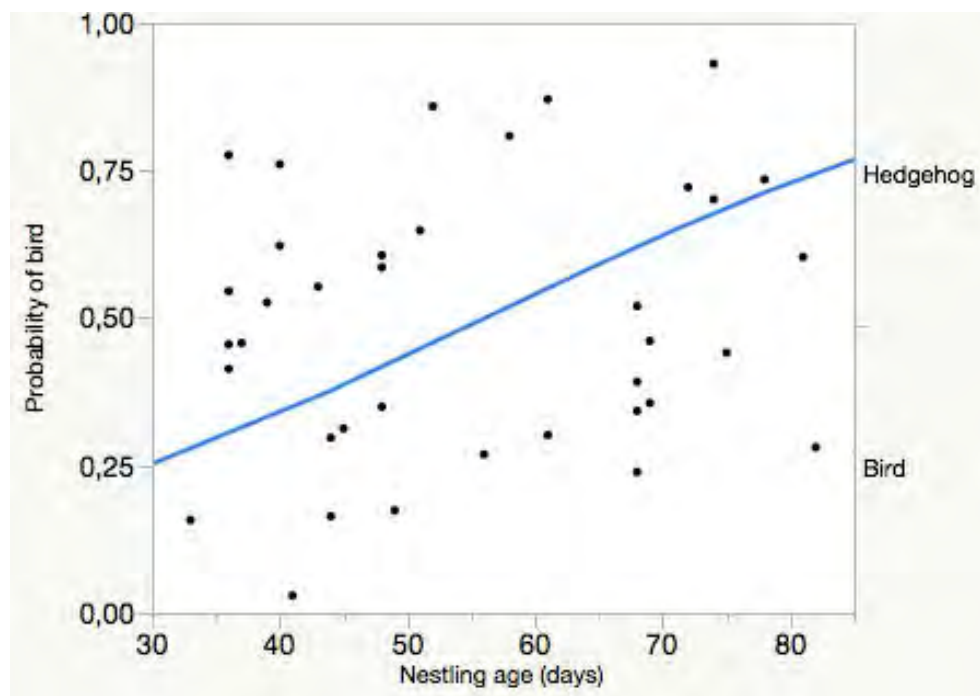| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	-2.969	1.458		4.15	0.041
Nestling age	0.047	0.024	1	3.58	0.058
Precipitation (mm)	0.192	0.116	1	2.71	0.099

Figure 7. The probability that a prey item delivered at the eagle owl nest was a bird, rather than a hedgehog, as a function of nestling age. Whole model: N = 37, x^2 = 3.33, df = 1, p = 0.067.

To reveal the factors that affected the probability that the prey item delivered was a duck rather than another bird, the following six explanatory variables were included in a full model and successively removed until only significant (p<0.05) or marginally non-significant (0.05<p<0.10) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, ambient temperature, precipitation and nestling age. Of these, time from solar midnight was kept in the final model as a marginally non-significant factor (Table 6). The probability that a delivered prey item was a duck, rather than another species of bird, increased with increasing deviation from solar midnight (Figure 8).

Table 6. Logistic regression model of the probability of a prey item delivered at the eagle owl nest was a duck. Whole model N = 44, x^2 = 6.01, df = 2, p = 0.049.

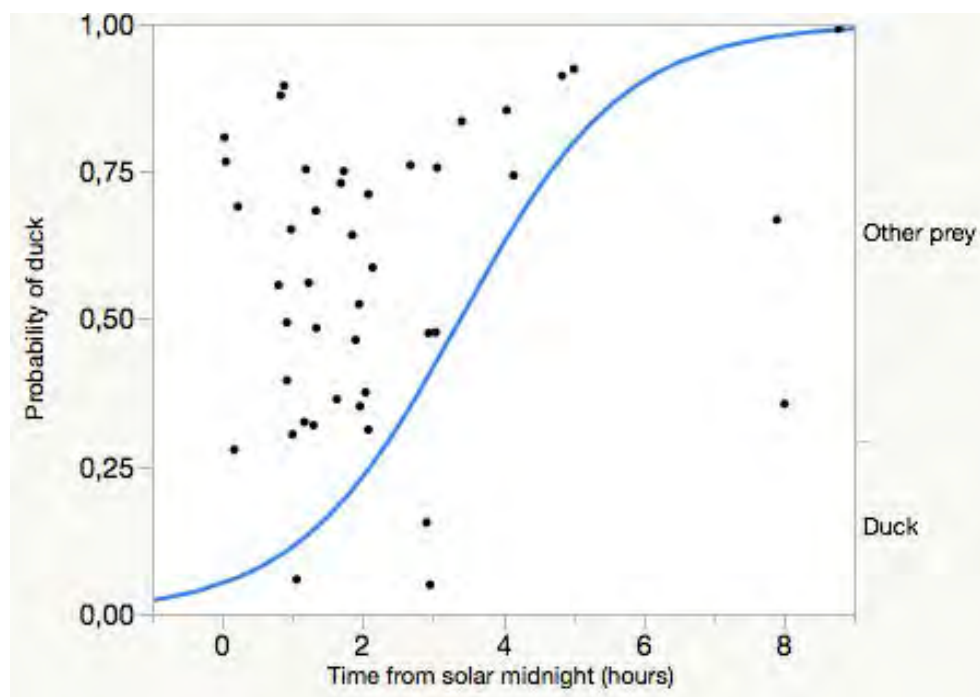| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	-2.915	1.283		5.16	0.023
Time from solar midnight	0.858	0.507	1	2.87	0.090

Figure 8. The probability of a prey item delivered at the eagle owl nest was a duck rather than another species of bird as a function of time from solar midnight. Whole model: N = 44 x^2 = 7.28, df = 1, p = 0.006.

Prey selection: successive items

To reveal the factors that affected the probability that the eagle owl was consistent when selecting between prey group (mammal, bird or amphibian) items, i.e. chose a prey item from the same prey group as the one delivered previously, the following six explanatory variables were included in a full model and successively removed until only significant ($p < 0.05$) or marginally non-significant ($0.05 < p < 0.10$) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, time elapsed since the previous delivery, precipitation, nestling age and ambient temperature. Of these, time from solar midnight was kept in the final model as a marginally non-significant factor (Table 7). The probability that the eagle owl was consistent when selecting between prey groups increased with increasing deviation from solar midnight (Figure 9).

Table 7. Logistic regression model of the probability that a prey item delivered at the eagle owl nest belonged to the same prey group as previous prey item delivered. Whole model N = 40, $x^2 = 3.76$, df = 1, p = 0.052.

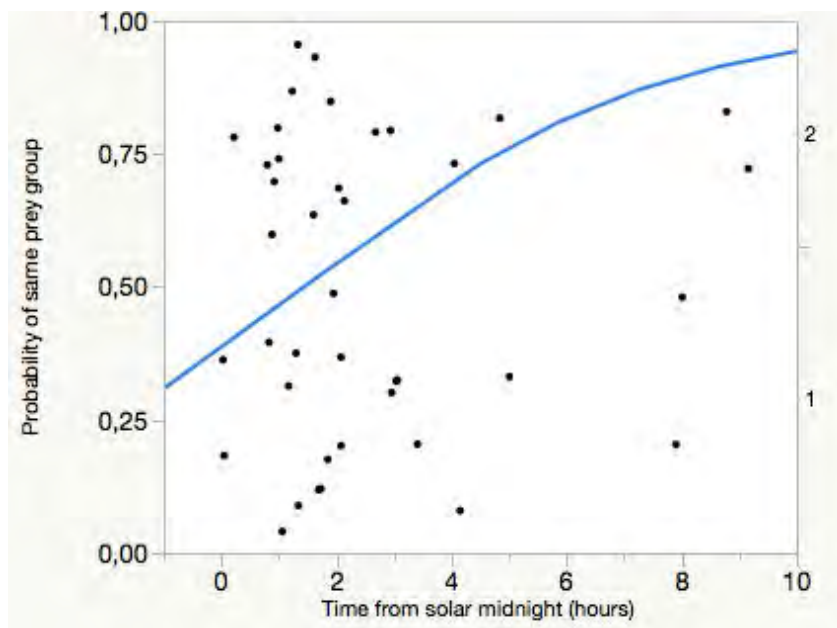| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	-0.476	0.536		0.79	0.374
Time from solar midnight	0.328	0.198	1	2.74	0.097

Figure 9. The probability that a prey item delivered at the eagle owl nest was of the same prey group as the previous prey item delivered, as a function of time from solar midnight. 1 = same prey group, 2 = different prey group. Whole model: N = 40 $x^2 = 3.76$, df = 1, p = 0.052.

To reveal the factors that affected the probability that the eagle owl was consistent when selecting between prey species, i.e. chose a prey species equal to the prey species delivered previously, seven explanatory variables were included in a full model and successively removed until only significant ($p<0.05$) or marginally non-significant ($0.05<p<0.10$) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, time elapsed since the previous delivery, precipitation, nestling age and ambient temperature. Of these, only whether the delivery was made before or after solar midnight were kept in the final model (Table 8). Further, the probability that the eagle owl was consistent when selecting between prey species, increased as the time elapsed since the previous delivery decreased (Table 9 & Figure 10).

Table 8. Likelihood ratio test of whether the probability that a prey item delivered at the eagle owl nest was of the same species as the previous item delivered, was affected by whether the delivery was made before or after solar midnight. Whole model N = 38, x^2 = 4.53, df 1, p = 0.033

Explanatory variable	df	x^2	p
Before/After solar midnight	1	4.54	0.033

Table 9. Logistic regression model of the probability that a prey item delivered at the eagle owl nest belonged to the same prey species as the previous prey item delivered. Whole model N = 37, x^2 = 8.15, df = 2, p = 0.016.

Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	-0.889	0.389		5.22	0.224
Time since previous delivery	0.784	0.389	1	4.05	0.044
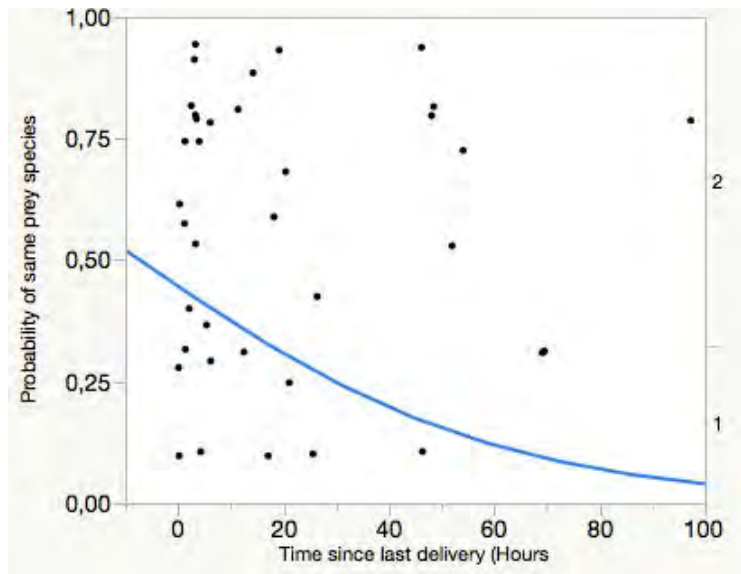
Figure 10. The probability that a prey item delivered at the eagle owl nest was of the same species as the previous prey item delivered, as a function of time since last delivery. 1 = same prey specie, 2 = different prey specie. Whole model: N = 37 x^2 = 2.82, df = 1, p = 0.092.

Prey handling prior to delivery

Birds were significantly more likely to be decapitated prior to delivery, than mammals (Figure 11). While no mammals was scored as decapitated, it was not possible to determine whether or not amphibians were decapitated, thus the latter were excluded from statistical tests of variables affecting the probability of prey items being decapitated prior to delivery.
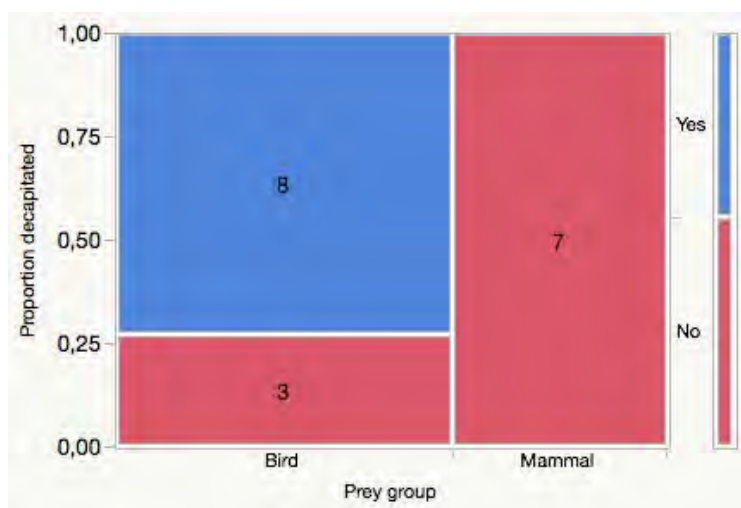
Figure 11. The proportion of avian and mammalian prey items delivered at the eagle owl nest that were decapitated prior to delivery, assigned to prey group. Whole model: N = 19, x^2 = 9.16, df = 1, p = 0.0025.

To reveal the factors that affected the probability that a bird was decapitated prior to delivery eight explanatory variables were included in a full model and successively removed until only significant (p<0.05) or marginally non-significant (0.05<p<0.10) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, ambient temperature, nestling age, precipitation, prey group and gross prey body mass. Of these, gross prey body mass were kept in the final model (Table 10). The probability that a bird was decapitated prior to delivery increased as prey body mass increased (Figure 12).

Table 10. Logistic regression model of the probability that a delivered prey bird was decapitated prior to delivery. Whole model: N = 11, x^2 = 4.43, df = 1, p = 0.0003.

Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	3.767	4.233		0.79	0.37
Gross prey mass	-0.018	0.017	1	1.23	0.27

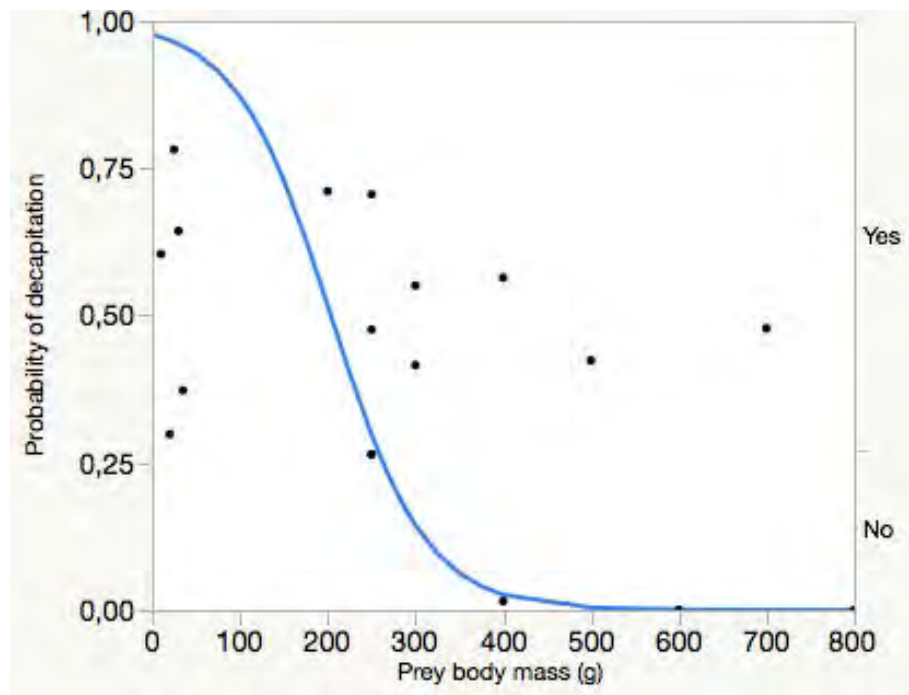
Figure 12. The probability that an avian prey delivered at the eagle owl nest was not decapitated prior to delivery, as a function of gross prey mass. At the right axis, Yes denotes decapitated, No denotes not decapitated. Whole model: N = 11, x^2 = 4.44, df = 1, p = 0.035.

Prey handling after delivery

To reveal the factors that affected the probability that nestlings fed on prey items unassisted, rather than the female dismembered the prey item and fed the morsels to the nestlings, the following seven explanatory variables were included in a full model and successively removed until only significant ($p<0.05$) or marginally non-significant ($0.05<p<0.10$) effects remained in the model: time from solar midnight, whether the delivery occurred before or after solar midnight, the interaction between the former two, gross prey mass, precipitation, nestling age and ambient temperature. Of these, the probability that the nestlings fed on prey items unassisted were significantly affected by nestling age and gross prey mass (Table 11). The probability that the nestlings fed unassisted increased as nestling age increased (Figure 13), and decreased as gross prey mass increased (Figure 14).

Table 11. Logistic regression model of the probability that the eagle owl nestlings fed on a prey item unassisted. Whole model N = 45, x^2 = 49.04, df = 2, p < .0001.

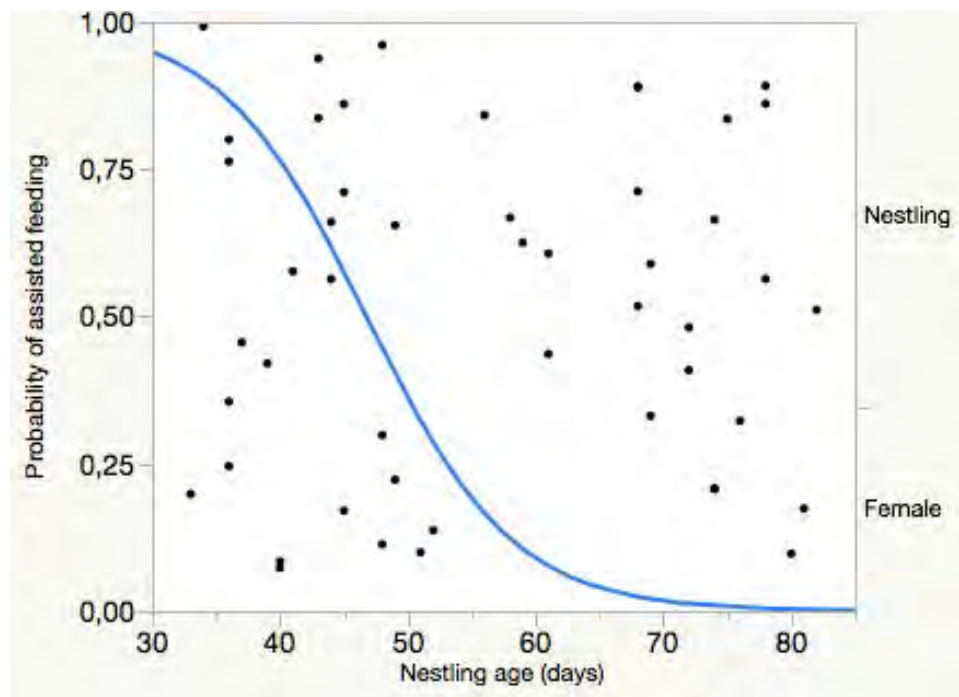| Explanatory variables	Estimate	Std Error	df	x^2	p
Intercept	11.805	6.139		3.70	0.054
Nestling age	-0.383	0.187	1	4.19	0.040
Gross prey mass	0.015	0.007	1	4.18	0.040

Figure 13. The probability that the nestlings fed on a prey items unassisted, as a function of nestling age. Whole model N = 49 x^2 = 29.44, df = 1, p < 0.001.
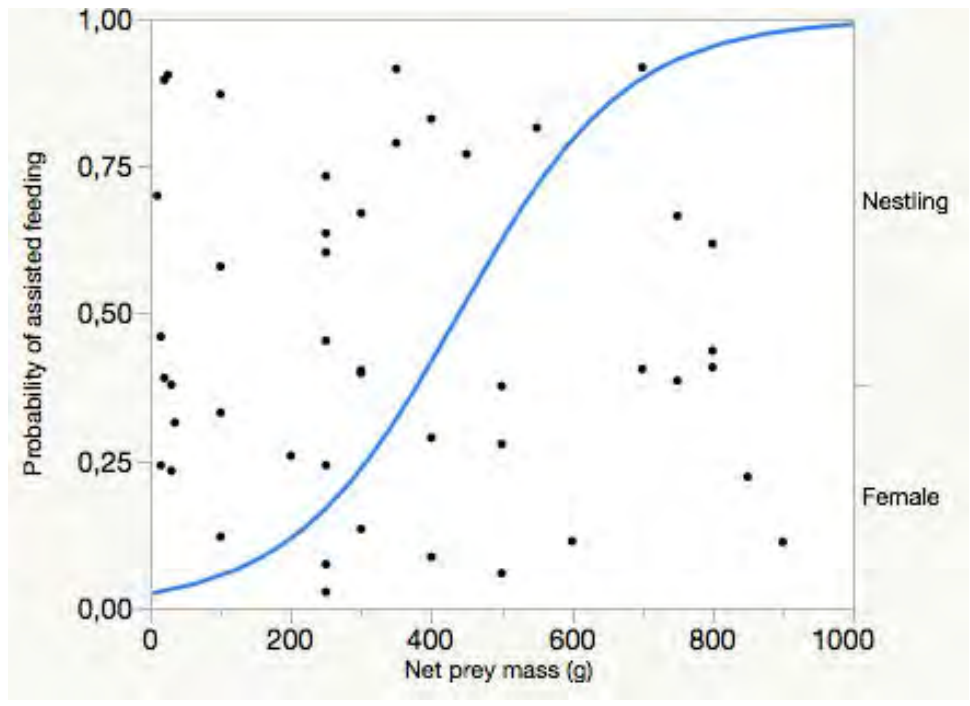
Figure 14. The probability that the nestlings fed on a prey item unassisted, as a function of gross prey mass. Whole model: N = 45, x^2 = 26.09, df = 1, p < 0.001.

Discussion

Prey delivered

A variety of prey was delivered at the nest during the period of monitoring. The diet was dominated by mammals and birds, which accounted for 53.1% and 36.7%, respectively, of 49 prey items. The most common mammal delivered was hedgehog, while the most common bird delivered was tufted duck. Amphibians accounted for paltry 2.0%. The low proportion of amphibians in the diet might be explained by the fact that amphibians are poikilothermic and requires certain temperatures to be active. In turn this could make them less vulnerable to eagle owl predation, as the eagle owl mainly hunts during hours where sunlight is absent (Papageorgiou et al. 1993). On the contrary, the hedgehog, which was the most abundant prey, is a nocturnal species, active during dusk and night (Semb-Johansson & Frislid 1990; Hubert et al. 2011). Whereas spines deter most predators, the eagle owl is among few species regularly killing hedgehogs by turning them over and opening their belly thank to their powerful talons (Cramp 1985; Hubert et al. 2011). Also, in addition to shared environment and circadian rhythm hedgehogs might be prone to predation because of lower escaping ability, as has been suggested for substandard water voles in northern Norway (Melis et al. 2011), making them a relative easy prey to capture. Where other prey are likely to flee when exposed to hazard, hedgehogs contracts muscles in their skin to roll up and form a protective ball-like shape where spines are turned outwards, often laying tirelessly for hours while waiting for the imminent danger to pass (Morris & Tjørve 1987; Semb-Johansson & Frislid 1990). A further factor that favour an abundance of hedgehogs in the study area is the cultural landscape, as hedgehogs are known to thrive near human activity and farms (Semb-Johansson & Frislid 1990). Results from a previous study confirms that availability of anthropogenic food sources (pet food) is a good predictor of adult hedgehog abundance (Hubert et al. 2011). As the eagle owl is known to specialize in the most advantageous prey (LourenÇo & Sergio 2006), it is likely for the monitored pair to have specialized in hedgehogs.

A preponderance of mammalian prey was also found in most previous studies of the eagle owl, both where results are drawn from collection of prey remains and pellet counts (Donazar et al. 1989; Amr et al. 1997; Marchesi et al. 2002; Penteriani et al. 2002; Shehab 2004; LourenÇo & Sergio 2006), and when they are based on video monitoring (Fosså 2013; Nielsen et al. 2015). As in my study, most of these studies (Marchesi et al. 2002; Sergio et al.

2002; LourenÇo & Sergio 2006; Fosså 2013; Nielsen et al. 2015) found mammal predominance in frequency of prey and in biomass delivered during breeding period.

In Greece, Papageorgiou et al. (1993) found a majority of avian prey in pellets from forest habitat, but a majority of mammalian prey in pellets from cultivated habitats, as well as in both habitats pooled. In Korea, Shin et al. (2013) found a dominance of avian prey in pellets from wetland habitat, but a majority of mammalian prey in pellets from non-wetlands. Further, in Norway Willgohs (1974) found a dominance of avian prey from analyses of pellets. However, data obtained from pellets or prey remains may be biased due to uncertainty in identifying prey species, or because few or no prey remains occur (Slagsvold et al. 2010). As for this study, recordings revealed that the female eagle owl frequently removed prey remains from the nest, thus, the diet composition would have appeared different if being analysed based on pellets and prey remains. The majority of avian prey in wetlands found by Shin et al. (2013), is likely a result of scarce presence of mammals in such habitat. Even though mammals are considered to be the eagle owl`s preferred prey, such findings nevertheless strengthens the perception of the eagle owl as a opportunistic generalist top-predator, possessing the ability to specialise on the most advantageous food source in its surroundings, enabling it to occupy several biomes (LourenÇo & Sergio 2006).

The dominance of mammalian prey could partly be explained by optimal foraging theory (MacArthur & Pianka 1966), predicting that predators should prefer the most profitable prey considering time spent hunting, prey body mass (i.e. energy intake) and handling time. While it is difficult to quantify the difference in time spent hunting between different prey items, my study provides data on body mass inequality among prey items. On average mammalian prey body mass was 444 g while avian species weighed on average 237 g, which was a significant difference in body mass. If handling time per mass unit is larger for avian prey than for mammalian prey (Slagsvold & Sonerud 2007; Slagsvold et al. 2010; Sonerud et al. 2014), the eagle owl should prefer large mammals rather than smaller birds. LourenÇo & Sergio (2006) suggests that lagomorphs is the most common eagle owl prey in Meditteranian habitats due to their body size and abundance. That larger prey items has been found to be ingested at a higher rate than smaller prey when parents feed nestlings (Steen 2010) further strenghtens this hypothesis. Further, I suggest that mammalian prey compared to avian prey requires less preparation prior to delivery, due to feathers and beak (i.e. decapitation) often needed to be removed from birds, providing parents more time to hunt and feed the young. Also, a majority

of mammals in the diet of the eagle owls that I studied, despite c. 2 km proximity of the nest to a nature reserve of rich bird abundance could further indicate a preference of mammalian prey. As shown by Oddane et al. (2012) eagle owl territories in Norway can exceed a range of 12 km^2 by far, thus making the birds avaliable as prey. However, this is speculative without mapping actual prey abundance in surrounding area or quantifying differences in time spent hunting different prey types, but should nevertheless be noted.

Mammals ranged in size from wood mouse (25 g) to hedgehog (mean estimate 570 g), while birds ranged in size from Eurasian siskin (10 g) to Eurasian curlew (700 g). Such span in prey sizes can be attributed to generalist and opportunist hunting behaviour, two assets enabling the eagle owl to hunt the most advantageous prey available (Papageorgiou et al. 1993; LourenÇo & Sergio 2006). Further, sit-and-wait predators are expected to predate a range of prey species, due to stochasticity in encounter rates (Melis et al. 2011). Consequently one must thereof consider the results as affected by the local availability of prey, and not exclusively as the preferred prey species of the eagle owl as a whole.

Hunting activity

While all prey items were delivered at the nest within 10 hours from solar midnight, the majority were delivered within 3 hours from solar midnight. This temporal distribution of prey deliveries is consistent with the perception of the eagle owl as a mainly nocturnal predator (Cramp 1985; Penteriani, Vincenzo et al. 2007; Fosså 2013; Øien et al. 2014; Nielsen et al. 2015). However, the eagle owl is known to occasionally hunt and deliver prey during bright daylight (Cramp 1985; Jacobsen & Røv 2007; Fosså 2013; Nielsen et al. 2015), as was also the case in my study. The ability to hunt during daylight was emphasized in a population of eagle owls residing in Lurøy municipality in northern Norway, close to the polar circle. Despite extensive hours of daylight during summer, thus the breeding season, the municipality covers the densest population in Norway, most likely also in the world (Jacobsen & Røv 2007). High numbers of water voles and absence of other vole predators, such as the American mink (*Mustela vison)*, are believed to cause ideal conditions for eagle owls in the area, illustrating their ability to adapt to different environmental conditions. As for my study area, short period of darkness during the night in the monitoring period may have forced the eagle owl to hunt occasionally during daylight. Also, as the eagle owl perch still for long

periods during hours of daylight, monitoring its territory, coincidences could also play a part if easily accessible prey were spotted during daylight.

Different prey types appeared to have different temporal distribution with regard to delivery at the nest. Hedgehogs were to a greater extent delivered during dusk and dawn than were rodents and birds, which more often were delivered during the darkest hours of the night. The circadian rhythm of hedgehogs, whose activity spans 8-10 hours from dusk till dawn (Semb-Johansson & Frislid 1990), is likely to explain its overrepresentation during twilight. Birds delivered in my study are diurnal. Thus attacking them at sleep, during the dark hours of night, when they are asleep, would increase the probability of a successful hunt, because predatory birds are typically larger than their prey and accordingly has a different flight performance (Hedenström & Rosén 2001). Further, as flight is energy demanding (Hedenstrom 1993), and as the eagle owl is a sit-and- wait ambush predator, aerial hunts, which is likely to follow if hunting waking birds, seems less rewarding. However, some alleged sightings has been made of the eagle owl hunting birds in the air (Cramp 1985; Jacobsen & Røv 2007). The rodents recorded as prey in my study, i.e. brown rat and wood mouse are both nocturnal, while sheltered during daylight (Semb-Johansson & Frislid 1990). Their higher frequencies as prey during dark hours are consequently expected considering the circadian rhythm of the eagle owl.

Prey selection

The probability that a delivered prey item was a hedgehog, rather than another prey type, decreased with increasing precipitation during the day of delivery. Despite extensive literature review I was unable to find any suggestion of avoidance from precipitation in hedgehogs. To the contrary, potential avoidance could prove to be counterintuitive as the common earthworm *(Lumbricus terrestris)*, which regularly are included in the diet of hedgehogs (Morris & Tjørve 1987; Semb-Johansson & Frislid 1990), tend to crawl out of the soil during and after rain (Chuang & Chen 2008), making them more accessible as prey. In turn this raises the question whether it is the hedgehogs that avoid rain, or if it is other prey species that increase their activity during rain that causes my result.

The probability that a delivered prey item was a hedgehog, rather than another prey type, decreased with increasing nestling age. Because eagle owl nestlings are more likely to ingest

prey items unassisted as age increase, and as prey body mass decrease (Sonerud et al. 2014), I suggest that prey items delivered before the nestlings were able to feed unassisted should be of high body mass (i.e. of high energy content), whereas traits that are unmanageable for nestlings, such as large size and spines can be assigned less importance. As for the provisioning parent, the ability to dissemble larger prey enables it to feed on and prepare prey of relative large size (Slagsvold et al. 2010), for instance a hedgehog. Such a potential strategy should increase delivery of hedgehog frequencies at low nestling ages, and decrease it at higher nestling ages. However, as nestling age corresponds to Julian date, the change in delivery rate of hedgehogs may also be an affect of seasonal change in the availability of hedgehogs.

The probability that a delivered prey item was a bird, rather than another prey type, increased with increasing nestling age. This may be a case of parents adjusting feeding effort and prey mass per delivery as nestlings grow. For the Eurasian kestrel (*Falco tinnunculus),* prey size has been found to decrease with increasing nestling age, possibly due to the necessity to provide older nestling with smaller prey when they start to feed unassisted, but their size-restricted swallowing capacity is still underdeveloped (Steen et al. 2012). In my study avian prey items weighed on average 237 g while mammalian prey items weighed on average 443 g, and the increase in avian prey in later nestling stages could hence be attributed to the upbringing of young where they learn to feed unassisted on unprepared prey items. Possible higher numbers of migratory birds and their offspring in later parts of the monitoring period could also have influence on the result.

The probability that a delivered prey item was a duck, rather than another species of bird, increased with increasing deviation from solar midnight, thus in lighter periods of the 24-hour day. The tufted duck in particular distinguished itself from other birds regarding timing of delivery. Because all ducks are known to be vigilant when sleeping (Zimmer et al. 2011), fewer attacks on ducks during the night could follow. But given the low sample size of ducks (n= 5) it is daring to suggest explanations of their presence during daylight. However, in Norway sightings has been made of eagle owls hunting aquatic birds (Willgohs 1974), presumably on water, thereof one could propose that birds on water have lower escape performance and thus are easier to catch during daylight than other birds.

Finally, two out of three delivered tufted ducks were delivered simultaneously, one by each parent, implying that a group of tufted ducks had been attacked, quite possibly by chance.

Prey selection: successive items

The probability that the eagle owl was consistent when selecting between prey groups increased with increasing deviation from solar midnight. Given that birds were delivered mainly at night a reasonable explanation could be that mammalian species, particularly the hedgehog, which were the dominant prey group and to a greater deal were delivered during lighter hours of the night, caused higher probability of successive hunts of the same prey group in hours that are deviated from solar midnight. Further, this would also clarify why the probability that the eagle owl was consistent when selecting between prey species was affected by whether it was before or after solar midnight, as different prey species had different temporal distribution of when to be delivered, due to difference in their activity patterns and their circadian rhythm.

The probability that the eagle owl was consistent when selecting between prey species, increased as the time elapsed since the previous delivery decreased. This result is an affect of high delivery frequencies of hedgehogs at early stages of monitoring. Sonerud (1985) suggest that clumped prey favours a win-stay strategy in predators. The win-stay strategy towards clumped prey should minimize the time elapsed between a successful hunt and a revisit to the same capture site. Single-prey loaded central place foraging birds, such as the eagle owls I monitored, are known to benefit from the win-stay strategy, indicating a strong spatial and topographical memory (Sonerud 1985). The hedgehog, which apparently was of high abundance in my study area, is likely to have favoured such a strategy.

Prey handling

Only birds were decapitated prior to delivery. That raptors tend to decapitate birds, more often than other prey types, has been found in previous studies as well (Steen 2010; Steen et al. 2010; Fosså 2013). The need to separate the head from the body of avian prey is believed to be due to large and sharp bills, considered inedible for nestlings (Steen et al. 2010). In my study, this is likely to be the case particularly for Eurasian woodcock, Eurasian curlew, hooded crow, black-headed gull and tufted ducks, which all have relative large bills. Also, a central place foraging, single-prey loader, such as the eagle owls that I studied, might decrease the load carried to the nest by removing inedible body parts such as feathers and head prior to delivering at nest, thus minimalizing energy spent on prey transport (Sodhi 1992).

The probability that an avian prey was decapitated prior to delivery at the eagle owl nest increased as prey body mass increased. As for the Eurasian kestrel, prey of larger body mass is more likely to be decapitated prior to delivery than prey of smaller body mass (Steen et al. 2010; Sonerud et al. 2013), presumably due to accompanying large heads with various obstacles, i.e. skull and bills, acting as feeding constraints for the nestlings, whose feeding techniques are poor and swallowing capacity is less developed. Further, as the preparing of food for dependent offspring among raptors is considered a trade-off between benefits for the nestling and costs for the parents as time spent on self-foraging is reduced (Steen et al. 2010), consuming the nutritious head of larger prey prior to delivery, will allow parents to spend more time on feeding themselves and broods, and less on provisioning (Rands et al. 2000).

The probability that the eagle owl nestlings fed unassisted increased as nestling age increased, and decreased as gross prey mass increased. This pattern has also been found for raptors in general (Sonerud et al. 2014). In passerine birds nestlings has been found to have difficulties swallowing large prey due to low swallowing capacity. This is termed the feeding constraint hypothesis, by Slagsvold and Wiebe (2007), who found the provisioning parents to solve this problem by increasing prey body mass per delivery as nestling age, and thus the swallowing capacity, increased. Consequently, in raptors, the feeding constraint hypothesis demonstrates how type and size of prey determines how long the female is confined to the nest provisioning for the young (Sonerud et al. 2014). In my study, in contrast to that of Slagsvold and Wiebe (2007), prey mass decreased as nestling age increased, mostly due to fewer hedgehogs in the latter stages of the breeding. The decrease in delivery of hedgehogs is likely due to the need of higher frequencies of smaller, more edible prey as nestling become expected to feed unassisted. Because the swallowing capacity is less of a constraint to raptors, which use their beak to slice killed prey into manageable parts (Slagsvold et al. 2010), the counterintuitive finding of decreasing prey body mass with increasing nestling age could be explained by the possible specialization towards hedgehogs, at lower nestling age.

Video monitoring as a method of studying raptor diet

Infrared motion-triggered cameras are widely used in vertebrate ecology, with application in avian nesting ecology among others (Swann et al. 2004). An obvious advantage of this method, as opposed to more traditional wildlife camera monitoring, is that one will not have to visit the nest to operate the recording equipment. Also, more traditional diet study methods, such as systematic collection of pellets and prey remains, have proven to be inadequate as they under- or over-estimates the frequency of different prey types, or otherwise provides an incomplete description of a raptor`s diet (Collopy 1983; Simmons et al. 1991; Mersmann et al. 1992; Sergio et al. 2002; Lewis et al. 2004). Such data may also be biased due to uncertainty in identifying prey species or because few prey remains occur (Slagsvold et al. 2010).

As for owls, diet analyses are commonly based on pellets, where bones, fur and feather fragments can be identified. This is neither time efficient nor precise (Nielsen et al. 2015). Sergio et al. (2002) found that studying pellets, rather than prey remains, gave a more realistic and diverse picture of the eagle owl`s diet, but failed to identify avian species which were found in prey remains at the nest. This suggests that a realistic estimate of the eagle owl`s diet is difficult to obtain without applying camera monitoring, which in turn should prove to be a conservation matter as the recognition and protection of food sources (i.e. hunting restriction) should be a measure in preserving raptors (Penteriani et al. 2002; LourenÇo & Sergio 2006).

However, equipment-associated problems did surface during my fieldwork and subsequent study. There was a period of three days when the equipment for reasons unknown failed to operate. Thus prey deliveries during this period were lost. Further, poor video quality or prey deliveries taking place beyond camera range, made identification of four prey items impossible. For the majority of raptor species the latter problem can be minimalized or avoided through an ideal mounting position of cameras, but for the eagle owl this problem is close to inevitable to occur to some degree, due to large nests and roaming nestlings (Cramp 1985). As for the occasionally poor video quality, this is likely to be temporary, as surveillance technology tends to improve over time.

The insufficiency described above is unlikely to exceed those of more traditional diet studies (pers. opinion). The level of precision is likely to be much greater applying video cameras,

mainly because the eagle owl was observed to regularly clear the nest for hedgehog remains, leaving no trace to follow if basing the diet study on pellets or prey remain.

Conclusions

Using video monitoring as a method to reveal actual frequencies of prey delivered at the nest provided detailed information of the breeding behaviour in the eagle owl. Mammals were the most common prey type delivered, followed by birds. The most common prey species delivered was the hedgehog, both by number and mass, which were so abundant as prey that specialization might be indicated. However, a mapping of prey density in the area would be required before one can make more reliable conclusions regarding preferred prey. Nestlings increased their ability to feed unassisted with age, which supports the feeding constraint hypothesis (Slagsvold & Wiebe 2007), claiming that poor swallowing capacity at younger age functions as a feeding constraint, consequently confining the feeding parent to the nest as sedentary processors of captured prey. To facilitate the ability of the nestlings to feed unassisted, the eagle owl parents delivered smaller prey, as nestling reached ages where they would be expected to handle prey themselves.

The video analysis enabled precise estimates in regard of the eagle owl`s diet, timing of delivery, and behaviour, which is difficult to obtain by the use of more traditional methods. However, to my knowledge only two nests of breeding eagle owls has been filmed for the purpose of mapping diet (Fosså 2013; Nielsen et al. 2015), making the data basis scarce. Hence, more data is required to claim the findings with greater confidence, and thus my findings should for now be treated with caution.

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Appendix

Appendix 1: Screenshot of the female eagle owl, dismembering and feeding a hedgehog to the nestlings. This is the first night of monitoring and the female appears curious to the newly mounted camera. Time and date appears in the right bottom of the frame.

Appendix 2: All hour-blocks of the day assigned to No (denotes number of current hour-block not containing prey delivery), Yes (denotes number of current hour-block containing at least one prey delivery), total number of each individual hour-block throughout period of monitoring, probability of delivery within current hour-block, and percentage given in percentage. Blank values in the two columns to the right are due to no prey deliveries.

Hour	No	Yes	Total	Probability	Percent
1	39	5	44	0.113	11.363
2	40	4	44	0.090	9.090
3	35	8	43	0.186	18.604
4	39	4	43	0.093	9.302
5	42	1	43	0.023	2.325
6	43	0	43	-	-
7	43	0	43	-	-
8	43	0	43	-	-
9	42	1	43	0.023	2.325
10	42	1	43	0.023	2.325
11	44	0	44	-	-
12	43	0	43	-	-
13	43	0	43	-	-
14	44	0	44	-	-
15	42	0	42	-	-
16	41	1	42	0.023	2.380
17	43	1	44	0.023	2.272
18	43	0	43	-	-
19	43	0	43	-	-
20	41	2	43	0.046	4.651
21	43	1	44	0.022	2.272
22	41	3	44	0.068	6.818
23	41	3	44	0.068	6.818
24	34	10	44	0.227	22.727

Appendix 3: Parameter estimates of a hedgehog being delivered throughout the day

Fixed effects:	Estimate	Std.Error	z value	p
(Intercept)	13.421	5.158	-2.602	0.009
I(cos(2 * pi * Hour/24))	14.652	7.73	1.895	0.058
I(sin(2 * pi * Hour/24))	-7.333	4.026	-1.820	0.068
I(cos(2 * 2 * pi * Hour/24))	-4.581	3.413	-1.342	0.178
I(sin(2 * 2 * pi * Hour/24))	8.912	4.34	2.053	0.04
I(cos(3 * 2 * pi * Hour/24))	0.211	1.071	0.197	0.84
I(sin(3 * 2 * pi * Hour/24))	-4.418	1.928	-2.291	0.021

Appendix 4: Parameter estimates of bird being delivered throughout the day

Fixed effects:	Estimate	Std.Error	z value	p
(Intercept)	-5.688	0.766	-7.425	<0.0001
I(cos(2	2.825	0.856	3.298	0.0009
I(sin(2	1.111	0.548	2.026	0.042

Appendix 5: Parameter estimates of a rodent being delivered throughout the day

Fixed effects:	Estimate	Std.Error	z value	p
(Intercept)	-5.564	0.596	-9.324	<0.0001
I(cos(2	1.238	0.756	1.636	0.10
I(sin(2	0.551	0.664	0.830	0.41