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Video monitoring reveals sexual differences in prey selection and prey handling in western marsh harriers (*Circus aeruginosus*) in Norway

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Abstract

A breeding population of marsh harriers (*Circus aeruginosus*) has established in SE Norway during the last decades, and the population is increasing. Yet, no study of the breeding ecology of this population has been conducted. I studied the diet, diel pattern of deliveries, and prey handling behavior of two nesting pairs of marsh harriers in SE Norway by video monitoring at the nests. A total of 1004 prey deliveries were recorded, and 948 of these were analyzed. All prey were vertebrates; 53.8 % were birds, 42.2 % were mammals, and the remaining 1.1 % of the identified prey were amphibians, fish and reptiles. The most numerous prey type was passerine birds (Passeriformes). Although these accounted for 51.3 % of the prey by number, they accounted for no more than 28.0 % of the mass delivered at the nests. The most important prey species, in terms of mass delivered at the nests, was the European water vole (*Arvicola amphibius*), which accounted for 24.5 % of the mass delivered. The probability of delivering a prey item in an hour block varied little during the daily activity period, but the probability of delivering an avian prey was highest in the afternoon, while the probability of delivering a mammalian prey was highest in the morning with an additional peak in the evening. Average prey body mass of the prey captured was 65.3 g, 87.0 g for mammalian prey and 48.0 g for avian prey. The male captured more passerines and smaller prey than the female, which could be linked to smaller size of the male than the female. The probability that a prey was decapitated prior to delivery at the nest increased with prey body mass and was higher for mammalian prey than for avian prey. For mammals, the probability that a prey was decapitated was affected by the age of the nestlings and which parent had captured the prey. For prey captured by the female, the probability that it was decapitated prior to delivery increased with nestling age, while opposite was the case for prey captured by the male. This is probably an effect of the changing hunting pressure when the female starts assisting the male in hunting in the latter part of the nestling period. The handling time increased with increasing prey body mass for both mammals and birds, but this increase was faster for mammalian prey, both when the female fed the nestlings and when the nestlings ingested prey unassisted. As the marsh harrier show functional response to prey, data from more nests and from more years, are needed to verify the trends found in my study.

Sammendrag

En bestand med hekkende sivhauk (*Circus aeruginosus*) har de siste tiårene etablert seg i Sørøst-Norge, og populasjonen øker stadig. Likevel har ingen studier blitt gjennomført på hekkebiologien til denne populasjonen. Jeg har analysert dietten, døgnmønster for byttedyrleveringer og behandling av byttedyr for to hekkende sivhaukpar i Sørøst-Norge gjennom videoovervåking av reirene. Av 1004 byttedyr som ble levert på reirene ble 948 analysert. Alle byttedyrene var virveldyr; 53.8 % var fugler, 42.2 % var pattedyr, mens de resterende 1.1 % av de identifiserte byttedyrene var amfibier, fisk og reptiler. Spurvefugler (Passeriformes) var den mest tallrike byttedyrgruppen. Selv om disse utgjorde 51.3 % av antallet byttedyr, utgjorde de ikke mer enn 28.0 % av den totale biomassen levert på reirene. Det viktigste byttedyret, i form av biomasse, var vånd (*Arvicola amphibius*), som utgjorde 24.5 % av all biomasse levert på reirene. Sannsynligheten for å levere et byttedyr til reiret varierte lite gjennom den aktive perioden av døgnet, men sannsynligheten for å levere en fugl var størst om kvelden, mens sannsynligheten for å levere et pattedyr var høyest på formiddagen og på kvelden. Gjennomsnittlig byttedyrvekt var 65.3 g, 87.0 g for pattedyr og 48.0 g for fugler. Hannen fanget mer spurvefugl og mindre bytter enn hunnen, som kan linkes opp mot at hannen er mindre enn hunnen. Sannsynligheten for at et bytte ble dekapitert før levering på reiret økte med byttedyrvekt og var høyrere for pattedyr enn for fugler. For pattedyr var sannsynligheten for at et bytte var dekapitert avhengig av alderen på ungene og hvilken av foreldrene som leverte byttet. For pattedyr fanget av hunnen økte sannsynligheten for at byttet var dekapitert med ungenes alder, mens det motsatte var tilfellet for pattedyr fanget av hannen. Dette er trolig en effekt av et endret jaktpress når hunnen begynner å assistere hannen i jakten mot slutten av hekkeperioden. Håndteringstiden økte med byttedyrvekt for både pattedyr og fugler, men økte raskere for pattedyr, både når hunnen matet ungene og når ungene spiste på egenhånd. Siden sivhauken viser funksjonell respons til endret byttedyrtetthet trengs det data fra flere reir og over flere år for å kunne verifisere funnene i mitt studie.

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Introduction

In most birds where the parents feed the nestlings, the prey items are swallowed whole, and thus require little handling. Prey selection by these birds are constrained by their swallow capacity (Moser 1986). Raptors, i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Stringiformes), have evolved feet to grip prey items and a sharp bill to tear the prey into smaller pieces, making them able to capture and ingest prey that are large relative to their own body size. Large prey are divided into small pieces, and the morsels swallowed are usually less than 3 g (Poole 1985, Wilmers et al. 2003). This results in extended handling time for raptors, and the handling time is expected to increase further when feeding nestlings, as the morsels must be small enough for the nestlings to ingest (Slagsvold & Sonerud 2007). Efficient feeding of the nestlings is important to reduce handling time and increase time for other activities, like brooding, hunting and self-feeding (Rands et al. 2000, Steen et al. 2010). Slagsvold and Sonerud (2007) suggested that the long mealtimes select for separate sex roles. If both parents hunt, the probability that one parent would arrive with prey while the other was still feeding the young would increase, and waiting in turn would delay the resumption of foraging (Slagsvold & Sonerud 2007). However, if one parent is specialized in hunting, and the other in partitioning prey to the nestlings, the food transfer from parent to offspring would increase (Slagsvold & Sonerud 2007). The female is confined to the nest for feeding the nestlings until they are physically capable of handling prey items unassisted (Newton 1979, Cramp & Simmons 1980). The female's confinement to the nest was found to depend on prey type and prey size (Sonerud et al. 2014a). Avian prey, with protruding parts like bill and feathers, require more handling and preparation, and will confine the female for a longer time than other types of prey that can be swallowed whole or need less preparation (Steen et al. 2010, Sonerud et al. 2013, 2014a, b). The different parental roles are thought to be related to the evolution of reversed sized sexual dimorphism (RSD) in raptors, where the females usually are larger than the males (Newton 1979). The degree of RSD among raptors has a large variation, and is suggested to be related to prey selection, where increased prey size and proportion of agile avian prey in the diet is related to increased RSD (Slagsvold & Sonerud 2007, Sonerud et al. 2014a).

The sexual dimorphism in the western marsh harrier (*Circus aeruginosus*), from now on termed marsh harrier, is moderate, with the female being 1.30 times heavier than the male and the wing length of females being 1.05 times longer than the males' (Cramp & Simmons 1980, Krijgsveld et al. 1998). The breeding range of the marsh harrier is in Western Palearctic, and it breeds in almost every country in Europe, but is absent from mountain areas and the subarctic parts of Fennoscandia (Hoyo & Collar 2014). It prefers to nest in shallow waters with extensive, tall standing reeds (*Phragmites*) and reedmace (*Typha*), and is thus benefitting from eutrophication and is expanding its breeding range (Cramp & Simmons 1980, Fløseth 2000, Cardador & Mañosa 2011). The diet of the marsh harrier consists of ground-living and marsh-living animals, in variety of classes, species and sizes, depending on the local circumstances (Schipper 1973). The main prey are usually birds and small mammals, but it can also include insects, frogs, snakes and fish (Hildén & Kalinainen 1966, Schipper 1973, Tornberg & Happala 2013). The size of prey included in the diet range from the smallest passerines (Passeriformes) at 9 g to adult mallards (*Anas platyrhynchos*) at over 1000 g (Tornberg & Happala 2013). Although being a well-studied species in Central Europe, no study of marsh harriers in Norway has been conducted, even after the marsh harrier established an increasing breeding population in Norway around year 2000, now counting >20 breeding pairs (Fløseth 2000, Heggøy & Øien 2014).

In this study, I used video monitoring at two marsh harrier nests to investigate the diet composition in the lowland area of southeast Norway, at the northern border of the distribution of marsh harriers. First, I wanted to analyze the diet in breeding marsh harriers. Second, I wanted to analyze patterns of prey deliveries at the nest, both daily and seasonal patterns. Third, I wanted to analyze the prey handling, both preparation prior to delivery at the nest and preparation at the nest. Handling time and the female's confinement to the nest is predicted to differ between prey type, prey size and nestling age. At last, I want to relate the diet and the prey handling to the different parental roles and RSD in marsh harriers.

Methods

Study areas

Locating nests was done by inquiring local ornithologists and searching the website artsobservasjoner.no to locate suitable nesting habitats for marsh harriers. I visited some relevant localities to search for nests. The exact location of a nest was determined after observing aerial prey transfer from the male to the female and observing that the female marsh harrier landed and took off from the same location a couple of times, indicating a nest. In the end, I located two nests that were suitable for study, one at the lake Hellesjøvannet and one at the lake Rokkevannet.

Hellesjøvannet is a hypereutrophic freshwater lake in Hellesjøvannet nature reserve located south in the municipality of Aurskog-Høland in Akershus county (59°44' N; 11°27' E) in Southeastern Norway. The area of the lake is 0.53 km^2, and the maximum depth is 2.1 m (Rørslett & Brandrud 1989). There is extensive stands of macrophytes like common reeds (*Phragmites australis*), water horsetail (*Equisetum fluviatile*) and lesser bulrush (*Typha angustifolia*) surrounding the lake. A mosaic of cultivated land and standing forest surrounds the nature reserve. The area is located in the boreonemoral vegetation zone (Moen 1988), and the standing forest is mainly dominated by Norway spruce (*Picea abies*) with some areas with deciduous forest.

Rokkevannet is a eutrophic freshwater lake in Rokke Landscape Protection Area located in Halden municipality in the county of Østfold (59°11′ N; 11°21′ E) in Southeastern Norway, approximately 75 km south of Hellesjøvannet. The area of the lake is 0.64 km^2 (Miljødirektoratet 2017). There is extensive stands of common reeds surrounding the lake, especially in the south end, where the reed zone is 100 m across. Rokke Landscape Protection Area is a part of a ground moraine formed during the last Ice Age, creating a landscape dominated by plains and gentle hills (Vestad 1998). Rokkevannet is surrounded by a mosaic of cultivated land, standing forest and clear-cut areas. The area is located in the boreonemoral vegetation zone (Moen 1988), the forest areas is dominated by Norway spruce, with Scots pine (*Pinus sylvestris*) in the dry, sandy areas and rich mix-forest around the lakes and streams.

Direct observations and video monitoring

I observed prey transfers from male to female outside the nest, as well as all deliveries to the nest in the field. I spent 136 hour of observing the marsh harriers directly. At Rokkevannet, this was done from a birdwatching tower at a distance at 350 m from the nest, for 97 hours, and at Hellesjøvannet from a parking lot situated approximately 400 m away from the nest, for 39 hours. The equipment used when observing was a Focus Naturescope with 20-60x zoom and an 85 mm lens as well as a Carl Zeiss Conquest HD 8x42 binocular. The birds seemed unaffected by my presence.

Permission to install video equipment was obtained from the landowners and the County Governor of Akershus. The video monitoring started on 19 June at Rokkevannet and on 24 June at Hellesjøvannet. The monitoring lasted until 29 July (40 days) and 21 July (26 days), respectively, equivalent to 24 hours after the last recorded prey delivery. The video monitoring resulted in 77,181 video clips, a total of 725 GB of data that had to be analyzed.

The method used for filming is a modification of that described by Steen (2009). For the filming, I used a charge-coupled device (CCD) camera with a wide-angle lens to get the best overview of the nest. At Rokkevannet the lens was switched to a zoom lens after five days due to accumulation of moisture on the lens and due to a long distance from the nest to the lens, resulting in poor image quality. This switch improved the image quality. Prey from these first five days (56 prey deliveries) were not identified, and are not included in the analyses. The camera was connected to a Digital Video Recorder (Secumate H.264 Mini Portable DVR) via a long video cable. The camera and mini-DVR used a 12-volt DC lead battery as a power source. A cable converter was used to reduce the voltage from 12 volts from the battery to 5 volts for mini-DVR. The DC lead battery was changed once a week to ensure continuous power supply. The Mini-DVR saved data on SD-cards and was stored in a waterproof plastic container which was placed under a tree outside the reed belt where the nest was located, about 30 m from the nest. Thus, I was able to replace the battery and change SD-card without disturbing the marsh harriers at the nest. The SD-cards used were SDHC Class 4 with 32GB of storage capacity. These were replaced every day to ensure continuous monitoring. Four cards were used, two in rotation at each nest. When changing SD-card I connected a small portable display to the mini-DVR, in this way I could manage the settings, if necessary, and test the system. The DVR was set to use the built-in motion sensor function (Video Motion Detector), only recording when there was movement in the selected sensitive area, which was set to the nest and the area immediately above to register when the adult marsh harriers entered and left the nest. The DVR was set to record the action 5 s prior to the triggering, and continued to record while the sensor was triggered and 10 s after triggering. This was done to ensure that the entering of the adults and the behavior of the nestlings before delivery was recorded, as well as prey handling at the nest. For further details of camera equipment, see Steen (2009).

In addition to visits for monitoring monitoring the camera equipment, the nest at Rokkevannet was visited three times; one to change the camera lens, one to ring the nestlings, and one to cut reed in front of the camera. The nest at Hellesjøvannet was not visited between the installation and the removal of the camera, the latter some weeks after the nestlings had left the nest.

Estimating nestling age

At both Rokkevannet and Hellesjøvannet, the brood consisted of 4 nestlings. The age of the nestlings was estimated based on their morphology. Geir A. Sonerud, Steve Moyes and Bernd Riedstra are all experts at raptors and the two latter has worked with marsh harriers for over 20 years. They estimated the age of the oldest nestling at Rokkevann on 19 June to be 10, 9 and 11 days, respectively. I used the mean and estimated the age of the nestlings to be 10 days old, i.e. hatching on 9 June. To estimate the age of the nestlings at Hellesjøvann I compared the developmental stage of the nestlings relative to the nestlings at Rokkevannet. I estimated the age of the nestlings on 24 June (first day of monitoring) to be the same age as at Rokkevannet on 1 July, i.e. 22 days, giving hatching on 2 June.

Identification of prey and estimating body mass

Each recorded delivered prey item at Rokkevannet after the lens was switched, and all recorded prey items at Hellesjøvannet, were identified to the lowest taxonomic level possible. Amphibians and reptiles were in general easy to identify because there are few species of these taxa in Norway. Small mammals could usually be identified based on their characteristics, in particular the relative length of the tail. Only 2.3 % of the rodents were impossible to identify to species. The avian prey were identified based on the plumage, if possible. However, birds not identified based on plumage, e.g. juvenile or plucked prey, were identified based on size and shape of their feet and beak. A few prey items (2.8 %) were impossible to identify as they were hidden behind the nestlings during the handling.

Identification was done by using VCL Media Player version 2.2.4 for Windows, playing the sequences repeatedly at a TV monitor or computer screen, frame by frame if needed, until identification could be done. For every prey delivered at the nests, the time of arrival of the delivering parent and the sex of the delivering parent were registered. The sex of the delivering parent was determined based on morphological features. A prey delivered by the female at the nest was defined as captured by the male if the female had been away from the nest for less than five minutes or screamed towards the sky after arrival at the nest, as a sign of communication with the male. If this was not the case, the prey was defined as captured by the female. A prey delivered by the male was defined as captured by the male, as female raptors never deliver prey to their mate.

There is relatively small intraspecific variation in the body mass of adult birds. Therefore I could use a mean body mass for each prey species obtained from data most relevant to the breeding season in Norway (Cramp 1985, 1988, 1992, Cramp & Perrins 1994, Selås 2001). This was controlled against unpublished data from migrating birds ringed at Akerøya Ornithological Station in 2015 and 2016. See Appendix 1 for the body masses used for each prey species in this study. For prey not identified to species, the body mass was still estimated. For unidentified passerines, I allocated the items into three groups based on the body size compared to prey identified to species. These groups were “small passerines” (12-20 g), “medium passerines” (20-30 g) and “thrush size” (70-80 g), where the body mass was set to 15 g, 25 g and 70 g, respectively. For avian prey classified to genus, the body mass was set as the average of the body mass of the relevant species.

These data were used for gross prey body mass, which was defined as the mass of the prey at the moment of capture. I also recorded signs of preparation, resulting in net prey body mass for each prey, which was defined as the mass at the moment of delivery at the nest. The net body mass was estimated corrected for decapitation and partial consumption of prey prior to delivery. For decapitated birds, I subtracted 12.9 % of the body mass, based on data from feeding raptors in captivity (T. Slagsvold & G.A. Sonerud, unpublished data). For partial consumed prey, I estimated the mass of the missing parts and the parts delivered at nest from the screen pictures.

For mammals, unlike birds, there is a relatively high intraspecific variation in body mass. To estimate the body mass of the mammalian prey, I compared the size of the prey with the toes of the adult or old nestling marsh harrier by the use of ruler on the monitor. Every rodent was given a head and body length xL, where x denotes the multiplication of the length of a toe of the marsh harrier on video, measured to nearest 0.5 x (table 1). Some specimens could not be measured, these were given the value “mean”, meaning the mean of all the measured specimens of that species. From these lengths, the mass of every specimen in all species could be estimated. As for birds, I recorded signs of preparation. Decapitated mammals were subtracted 16.5 % of the body mass (Sonerud et al. 2014a) and for partial consumed prey, I estimated the mass of the missing parts and the parts delivered at the nest from the picture on the monitor. The body mass of the different mammalian species were estimated with a separate method for each species, as following below.

Table 1: Length of rodents, compared to marsh harrier toes, delivered at marsh harrier nests at Hellesjøvannet (a), Rokkevannet (b), and in total (c).

Species	N	Variation	Median	Mean	SE
a)					
Water vole excl. "mean"	161	1.5-7.0	3.5	3.56	0.067
Water vole incl. "mean" *	167	1.5-7.0	3.5	3.55	0.066
Field vole	15	2.0-4.0	2.5	2.67	0.135
Bank vole	1	2.5-2.5	2.5	2.5	-
Apodemus sp. excl. "mean"	25	2.0-3.0	2.5	2.28	0.058
Apodemus sp. incl. "mean" *	30	2.0-3.0	2.5	2.31	0.051
Brown rat	1	5.0-5.0	5.0	5.0	-
b)					
Water vole	65	2.5-7.0	4.0	4.00	0.129
Bank vole	39	1.5-4.5	2.5	2.61	0.107
Apodemus sp. excl. "mean"	53	1.0-3.0	2.5	2.39	0.058
Apodemus sp. incl. "mean" *	54	1.0-3.0	2.5	2.39	0.057
c)					
Water vole excl. "mean"	223	1.5-7.0	3.5	3.68	0.062
Water vole incl. "mean" *	232	1.5-7.0	3.5	3.68	0.061
Field vole	54	1.5-4.5	2.5	2.62	0.085
Bank vole	1	2.5-2.5	2.5	2.5	-
Apodemus sp. excl. "mean"	78	1.0-3.0	2.5	2.35	0.044
Apodemus sp. incl. "mean" *	84	1.0-3.0	2.5	2.36	0.041
Brown rat	1	5.0-5.0	5.0	5.0	-

* Rodents given "mean" length from video is given median length in this calculation.

European water vole (*Arvicola amphibius*)

The body mass of European water voles, hereafter termed water vole, was obtained from two sources. First, water voles captured in snap traps in Øyer in Oppland county in Norway, and later given as prey to raptors in captivity for rehabilitation after an accident (n = 13), had a body mass ranging from 38 g to 152 g, with a mean of 89 g (SE = 9.0 g) and median of 92 g (H.E. Grønlien & G.A. Sonerud, unpublished data). Second, live-captured water voles (n = 248) at Sleneset in Nordland county in Norway had body mass ranging from 42 g to 212 g, with a mean of 101 g (median not given; Melis et al. 2011). From these data I decided that a median water vole (3.5 L) captured by a marsh harrier would weigh 100 g. Then every unit of L was set to 30 g, so the body mass of a water vole with maximum length (7.0 L) was estimated to be 205 g, while the body mass of a water vole with minimum length (1.5 L) was estimated to be 40 g (table 2). The relation between body mass and length used for water voles was also used for the only brown rat (*Rattus norvegicus*) captured by the marsh harriers.

Field vole (*Microtus agrestis*)

The body mass of field voles was obtained from two sources. First, field voles captured in snap traps in April 1993 – 2016 in Ås in Akershus county in Norway (n = 9) had a body mass ranging from 23 g to 38 g, with a mean of 32 g (SE = 1.4 g) and a median of 33 g (G.A. Sonerud, unpublished data). Second, field voles captured in snap traps in October 1993 – 2016 in Ås in Akershus county in Norway (n = 7) had body mass ranging from 17 g to 36 g, with a mean of 24 g (SE = 2.4 g) and a median of 24 g (G.A. Sonerud, unpublished data). From these data, the body mass of a field vole with median length (2.5 L) captured by a marsh harrier in June-July was set to be 28 g. Every unit of L was set to be 10 g, so the estimated body mass of a field vole with maximum length (3.5 L) was set to 38 g, while the body mass of a field vole of minimum length (1.5 L) was set to be 18 g (table 2).

Bank vole (*Myodes glareolus*)

The body mass of bank voles was obtained from two sources. First, bank voles captured in snap traps in April 1993 – 2016 in Ås in Akershus county in Norway (n = 103) had a body mass ranging from 13 g to 30 g, with mean of 22 g (SE = 0.3 g) and a median of 22 g (G.A. Sonerud, unpublished data). Second, bank voles captured in snap traps in October 1993 – 2016 in Ås in Akershus county in Norway (n = 519) had a body mass ranging from 11 g to 29 g, with mean of 17 g (SE = 0.1 g) and a median of 17 g (G.A. Sonerud, unpublished data). Based in these data, the body mass of a bank vole with median length (2.5 L) captured by a marsh harrier in June-July was estimated to be 20 g (table 2).

Mice (*Apodemus* sp.)

The body mass of mice was obtained from two sources. First, wood mice (*Apodemus sylvaticus*) captured in snap traps in April 1993 – 2016 in Ås in Akershus county in Norway (n = 53) had a body mass ranging from 19 g to 32 g, with mean of 26 g (SE = 0.4 g) and a median of 25 g (G.A. Sonerud, unpublished data). Second, wood mice captured in snap traps in October 1993 – 2016 in Ås in Akershus county in Norway (n = 675) had a body mass ranging from 7 g to 30 g, with mean of 18 g (SE = 0.1 g) and a median of 18 g (G.A. Sonerud, unpublished data). Based on these data the body mass of an *Apodemus* mice with median length (2.5 L) captured by a marsh harrier in June-July was set to be 23 g. Every unit of L was set to be 10 g, so the estimated body mass of a mice with maximum length (3.0 L) was set to 28 g, while the body mass of a mice of minimum length (1.5 L) was set to be 13 g (table 2).

Table 2: Estimated body mass of rodents delivered at two marsh harrier nests, obtained by comparing the rodents' body length to the toes of the adult or old nestling marsh harrier by video.

	Estimated body mass (g)			
Body length relative to a marsh harrier toe	Water vole	Field vole	Bank vole	*Apodemus* sp.
1.5	40	18		13
2.0	55	23		18
2.5	70	28	20	23
3.0	85	33		28
3.5	100	38		
4.0	115			
4.5	130			
5.0	145			
5.5	160			
6.0	175			
6.5	190			
7.0	205			

Mountain hare (*Lepus timidus*)

The body mass of the complete mountain hares delivered by the marsh harriers (n = 2) was estimated by a comparison of their size with the size of the largest water voles captured (estimated to 205 g), and was set to 200 - 250 g. However, most of the hares were partially consumed. For these prey, I compared the size of the parts delivered with the size of other mammalian prey delivered at the nest, and estimated both net body mass and gross body mass. Net body mass of these prey was estimated to 30 - 350 g, with the gross body mass ranging from 200 to 800 g.

Fish

The body mass of fish was estimated with a standard weight-length relationship formula $W = aL^b$, where W is the body mass of the fish and L is the length of the fish, recommended by Froese (2006). The coefficients a and b have a species-specific value found at fishbase.org (table 5). The length of the fish was estimated with the same method as used for the rodents; they were compared with the middle toe of the female marsh harrier. Measurements of four museum specimens of marsh harriers at Natural History Museum in Oslo (NHM) were done to control the length of the marsh harrier toe.

Table 3: The a and b values for the fish species delivered at the marsh harrier nest at Hellesjøvannet, used to estimate body mass. The values was gathered from fishbase.org (Froese 2006, Froese et al. 2014)

Species	a	b
Common bream (*Abramis brama*)	0.00871	3.14

Handling time

Handling time of a prey item, defined as preparation at the nest done by the female or the nestlings, partitioning by the female, and unassisted feeding by the nestlings, was estimated for each prey delivered at the nests where the female partitioned, and for every fifth prey where the nestlings fed unassisted. The handling time was measured to the nearest s. I used the same definition of handling time as Steen (2010) did for the Eurasian kestrel (*Falco tinnunculus*), namely the time elapsed from when the female or nestling bent its head down towards the prey item to tear off the first piece of the prey, until the prey item was completely consumed. If the feeding paused for more than 5 s, I subtracted this pause from the total handling time. Handling time, by definition, includes time spent capturing prey and preparing the prey prior to delivering at nest, but this is not included in my study, because preparation outside the nest was seldom observed and because the marsh harriers were not observed while hunting. Handling time was estimated for 242 prey items where the female assisted the nestlings and for 121 prey items where the nestlings fed unassisted.

Statistical analysis

Statistical analysis were performed, and figures were designed, in the software programs JMP® version 13.0.0 (SAS Institute Inc. 2015) and R version 3.3.3 (R Development Core Team 2014). In R version 3.3.3 the packages “lme4” (Bates et al. 2014) and “AICcmodavg” (Mazerolle 2016) were used to conduct mixed-effect models. I used backward elimination as a standard method in order to find the final models and the standard criterion for eliminating variables was set to $\alpha = 0.05$. Only prey items of the classes Aves and Mammalia were included in the analyses, as the other classes were represented by low numbers.

I used logistic regression to test for effects of selected variables on the response whether the female or the male had captured the prey, and whether the female or male delivered the prey at the nest. The variables tested were gross prey body mass, prey class, age of the nestlings, and all interactions between these variables. I also used logistic regression to test for effects of different variables on the responses whether the male delivered the prey to the female outside the nest or delivered the prey directly to the nestlings at the nest, and whether a prey delivered at the nest by the female was captured by the female. The explanatory variables tested were gross prey body mass, prey class, age of the nestlings, and all interactions between these variables.

Logistic regression was also used to test whether the prey items were decapitated or not, prior to delivery at the nest. Prey body mass, prey class, age of the nestlings, which parent had captured the prey, and all possible interactions were tested as variables. To test whether the parent providing the prey to the nest should be included in the models I did a contingency analysis to test if the female prepared the prey transferred from the male outside the nest. I used logistic regression to test which variables affected the probability that an avian prey rather than a mammalian prey was delivered. The variables tested in this model was time of day and age of the nestlings.

Whether the nestlings fed unassisted or were assisted by the female was also tested by logistic regression by likelihood ratio. The explanatory variables tested were prey class, net prey body mass, nestling age, and all interactions between these variables. Inverse prediction with a 0.5 probability was used in the model to predict the age at which the nestlings would become more likely to ingest the prey unassisted rather than to be assisted by the female.

I used generalized linear models (GLM) to test for effects of explanatory variables on handling time when the female fed the nestlings and when the nestlings fed unassisted. Handling time and net prey body mass were $\log_{10}$-transformed to obtain normal distributed residuals from the final models. The explanatory variables included were prey class, net prey mass ($\log_{10}$), age of the nestlings, and the possible interactions between these variables. Whether the prey item was decapitated or not prior to delivery was not included in the models, for both statistical and biological reasons; only large prey items were decapitated, and these were few. The model including the variable decapitation had a lower Akaike information criterion (AIC = 86.10) than the model excluding decapitation (AIC = 87.08), indicating a better model. However, the difference in AIC was less than 2.0 and I chose to keep the simpler model, not including decapitation (Burnham & Anderson 2002). I also used GLM to test whether nestling age or nestling age squared affected the prey mass delivered at the nest per nestling per day.

I used generalized mixed effect models (GLMM) to the analyses of activity rhythm, performed in R. The periodic components of time series were set as sine and cosine functions in order to analyse the circadian activity rhythm (Pita et al. 2011). I used the cosinor method to adopt the fixed explanatory variable “time of day” (Pita et al. 2011). The day was divided into 24 hour blocks, and each hour block was used as sample unit, and termed x in the models. The probability of a prey being delivered at the nest within an hour block was set to be the response variable. If one or more prey deliveries within an hour block was observed it was scored as “yes”, and if there were no prey deliveries within an hour block, it was scored as “no”, making this a conservative test. This was scored for deliveries of mammalian prey and avian prey separately. The activity models were specified as follow:

$$M_1: logit\big(f(x)\big) = a_0 + \varepsilon$$

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

$$M_3: logit\big(F(x)\big) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2\cdot 2\pi x}{24} + b_{21} \sin\frac{2\cdot 2\pi x}{24}\right) + \varepsilon$$

$$M_4: logit\big(F(x)\big) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2\cdot 2\pi x}{24} + b_2 \sin\frac{2\cdot 2\pi x}{24}\right) + \left(a_3 \cos\frac{3\cdot 2\pi x}{24} + b_3 \sin\frac{3\cdot 2\pi x}{24}\right) + \varepsilon$$

Each model fit (M_1-M_4) was evaluated by assessing AICc values. The model fit was ranked in accordance with the AICc values, with a difference in AICc (ΔAICc) from the best model of 2.0 as the critical value for separating the model with the best fit (Burnham & Anderson 2002).

Results

Prey delivered at the nests

In total 1004 recordings of prey deliveries were made at the two marsh harrier nests during the monitoring period. At Rokkevannet 595 prey items were recorded delivered, while 409 prey items were recorded delivered at Hellesjøvannet. Of these, 948 items were analyzed and identified to the lowest taxonomic level, but 27 of these (2.8 %) were not possible to identify. Of the remaining, 288 were classified to order only, 82 to family only, 132 to genus only and 419 were classified to species. Of the prey items delivered (table 4), 53.8 % were birds, 42.2 % were mammals, 0.8 % were amphibians, 0.2 % were fish, and one prey item, 0.1 %, was a reptile, a viviparous lizard (*Lacerta vivipara*).

A total of 510 prey items were classified to birds, with passerines as the most important order with 486 items. In total 24 avian species were identified, ranging in size from *Phylloscopus* warblers to mallards and common pheasants (*Phasianus colchicus*). Yellowhammer (*Emberiza citrinella*) was the most common bird species, followed by common blackbird (*Turdus merula*) and common reed bunting (*Emberiza schoeniclus*). However, most birds (281) were classified as unidentified passerines, these were grouped according to size, i.e. small, medium and larger passerines (see methods). The most numerous avian order other than passerines were ducks (Anseriformes), with a total of 15 specimens. The average mass of avian prey was 48.0 ± 5.5 g, with a median mass of 16 g, while the average mass of mammalian prey was 87.0 ± 4.0 g, with a median mass of 85 g.

Of the 400 mammalian prey identified, water vole was the most common prey by number with 232 items (58.0 %), and the most contributing to total mass delivered at the nests, with 21,577 g (Appendix 2), counting for 45.0 % of the total mass of 47,915 g delivered to the nests. The average gross body mass of prey was 65.3 ± 3.6 g, whereas the average net body mass of prey delivered at nest was 52.2 ± 1.8 g.

Table 4: Number of prey items recorded delivered at two marsh harrier nests in Norway by use of video, given as percentage by number for each prey category.

Prey	Rokkevannet		Hellesjøvannet		Total	
	N	%	N	%	N	%
Mountain hare (*Lepus timidus*)	19	3.5	0	0.0	19	2.0
Mice (*Apodemus* sp.)	54	10.0	30	7.3	84	8.9
Brown rat (*Rattus norvegicus)*	0	0.0	1	0.2	1	0.1
Bank vole (*Myodes glareolus)*	0	0.0	1	0.2	1	0.1
Field vole (*Microtus agrestis)*	39	7.2	15	3.7	54	5.7
European water vole (*Arvicola amphibius*)	65	12.1	167	40.8	232	24.5
Unidentified rodents	8	1.5	1	0.2	9	0.9
Mammals total	185	34.3	215	52.6	400	42.2
Mallard (*Anas platyrhynchos)*	2	0.4	1	0.2	3	0.3
Duckling (Anatidae indet.)	10	1.9	2	0.5	12	1.3
Common pheasant (*Phasianus colchicus*)	2	0.4	0	0.0	2	0.2
Common moorhen (*Gallinula chloropus*)	0	0.0	1	0.2	1	0.1
Rail (Rallidae indet.)	0	0.0	1	0.2	1	0.1
Common swift (*Apus apus*)	1	0.2	0	0.0	1	0.1
Pigeon (Columbidae indet.)	4	0.7	0	0.0	4	0.4
Eurasian skylark (*Alauda arvensis*)	1	0.2	2	0.5	3	0.3
European robin (*Erithacus rubecula*)	2	0.4	0	0.0	2	0.2
Whinchat (*Saxicola rubetra*)	1	0.2	1	0.2	2	0.2
Common blackbird (*Turdus merula*)	3	0.6	7	1.7	10	1.1
Fieldfare (*Turdus pilaris*)	2	0.4	6	1.5	8	0.8
Redwing (*Turdus iliacus*)	1	0.2	0	0.0	1	0.1
Song thrush (*Turdus philomelos*)	0	0.0	8	2.0	8	0.8
Thrush indet. (*T. philomelos* or *T. iliacus*)	11	2.0	28	6.8	39	4.1
Eurasian blackcap (*Sylvia atricapilla*)	3	0.6	1	0.2	4	0.4
Garden warbler (*Sylvia borin*)	0	0.0	3	0.7	3	0.3
Warbler (*Sylvia* sp.)	2	0.4	4	1.0	6	0.6
Warbler (*Phylloscopus* sp.)	5	0.9	28	6.8	33	3.5
Warbler (Sylviidae indet)*	6	1.1	18	4.4	24	2.5
Great tit (*Parus major*)	3	0.6	1	0.2	4	0.4
Tit (*Poecile montanus or P. palustris*)	0	0.0	1	0.2	1	0.1
Eurasian jay (*Garrulus glandarius*)	0	0.0	1	0.2	1	0.1
Hooded crow (*Corvus cornix*)	2	0.4	1	0.2	3	0.3
Eurasian tree sparrow (*Passer montanus*)	5	0.9	1	0.2	6	0.6
Common chaffinch (*Fringilla coelebs*)	2	0.4	2	0.5	4	0.4
European greenfinch (*Chloris chloris*)	0	0.0	3	0.7	3	0.3
Common reed bunting (*Emberiza schoeniclus*)	5	0.9	3	0.7	8	0.8
Yellowhammer (*Emberiza citrinella*)	18	3.3	14	3.4	32	3.4
Unidentified passerines	233	43.2	48	11.7	281	29.6
Passerines total	305	56.6	181	44.3	486	51.3
Birds total	325	60.3	185	45.2	510	53.8
Frog (*Rana* sp.)	7	1.3	1	0.2	8	0.8
Amphibians total	7	1.3	1	0.2	8	0.8

Viviparous lizard (*Lacerta vivipara*)	1	0.2	0	0.0	1	0.1
Reptiles total	1	0.2	0	0.0	1	0.1
Common bream (*Abramis brama*)	0	0.0	2	0.5	2	0.2
Fish total	0	0.0	2	0.5	2	0.2
Unidentified prey	21	3.9	6	1.5	27	2.8
Total	539	100.0	409	100.0	948	100.0

* Using the old classification of Sylviidae, including *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*.

The probability that an item delivered at the nest was an avian prey, rather than a mammalian prey, was significantly affected by the time of the day and the age of the nestlings (table 5). The probability of avian prey increased during the day, and decreased as the nestlings became older (figure 1).

Table 5: Parameter estimates from a logistic regression model of the probability that a prey item delivered at the nest was an avian prey rather than a mammalian prey (n = 910).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	-0.679	0.350	3.78	0.052
Nestling age	-0.030	0.008	13.57	<0.001
Time of day	0.042	0.016	7.02	0.008

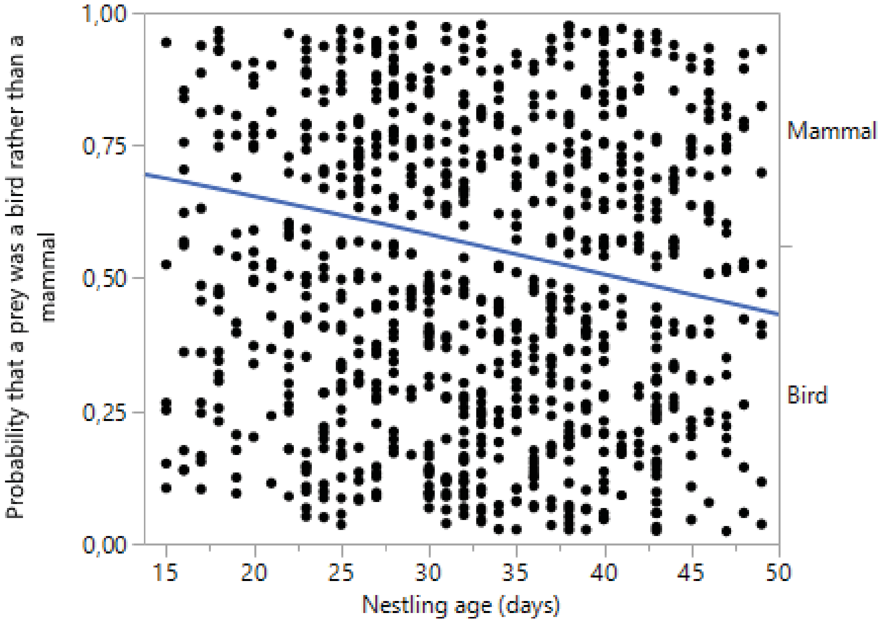

Figure 1: The probability that a prey delivered at the nest was an avian prey, rather than a mammalian prey, as a function of the age of the nestlings (n = 910).

From the cosinor analysis, the probability of a prey item being delivered at the nest as a function of time of day was best explained by model M_4, with the loweset AIC value, for both mammalian prey and avian prey (table 6). The parameter estimates of the best model is given in Appendix 4 and 5. Prey items were delivered at the nest between 05.00 and 23.00 hours, with one exception, one item was delivered at 04.50. The probability of an avian prey item being delivered at the nest increased during the day and was peaked during the hour blocks between 16.00 and 19.00, while the probability of a mammalian prey item being delivered at the nest peaked during the hour blocks between 07.00 and 13.00, with a second peak in the hour block between 18.00 and 19.00 (figure 2).

Table 6: Output from the cosinor analysis performed in R, of the best models for the probability that a) a mammalian prey and b) an avian prey was delivered at two marsh harrier nests as a function of the time of day. For parameter estimates of the best models, see Appendix 4 and 5.

Model	df	AIC	ΔAIC
M_{4a}	7	1375.57	0.00
M_{3a}	5	1396.83	21.26
M_{2a}	3	1465.51	89.93
M_{1a}	1	1661.16	285.58
M_{4b}	7	1414.64	0.00
M_{3b}	5	1417.75	3.11
M_{2b}	3	1511.72	97.08
M_{1b}	1	1778.91	364.27

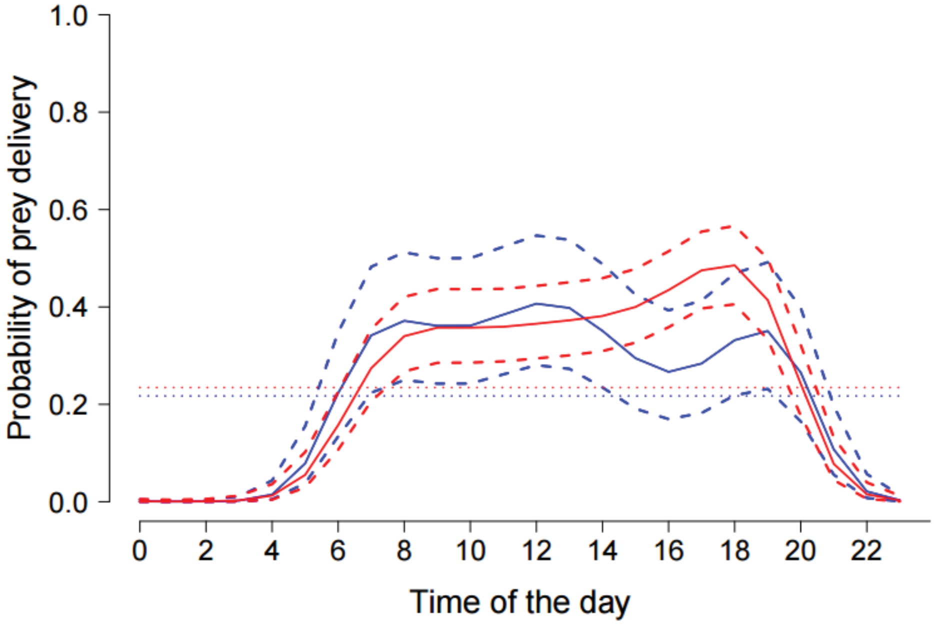

Figure 2: Result from generalized mixed effect models (GLMM), performed in R, on the probability that a prey item was delivered at two marsh harrier nests as a function of time of day. The blue line represent mammalian prey, while the red line represent avian prey. The figure is based on the best models, M_{4a} and M_{4b}, for mammalian and avian prey, respectively, derived from the cosinor analysis; see table 6 and appendix 4 and 5 (n = 1622).

At the two nests, on average 15.5 ± 0.7 prey items were delivered per day, giving 3.9 ± 0.2 prey per nestling per day. The average prey mass delivered per day was 765 ± 40 g, or 191 ± 10 g per nestlings per day. The average prey mass delivered per nestling per day was significantly affected by the age of the nestlings squared (table 7).

Table 7: Parameter estimates from a generalized linear model (GLM) of significant effects on prey mass delivered at nest per nestling per day at two marsh harrier nests in Norway (n = 35).

Explanatory variable	Estimate	SE	t	p
Intercept	-175.641	85.834	-2.05	0.049
Nestling age	25.762	5.717	4.51	<0.001
Nestling age^2	-0.406	0.088	-4.59	<0.001

The prey mass delivered per nestling per day increased from the first day of recording, until the age of the nestlings reached 31.5 days ($f'(-175.641+25.762x-0.406x^2 = 0)$). After the maximum point the prey mass delivered at the nest per nestling per day decreased until prey was no longer delivered at the nest (figure 3).

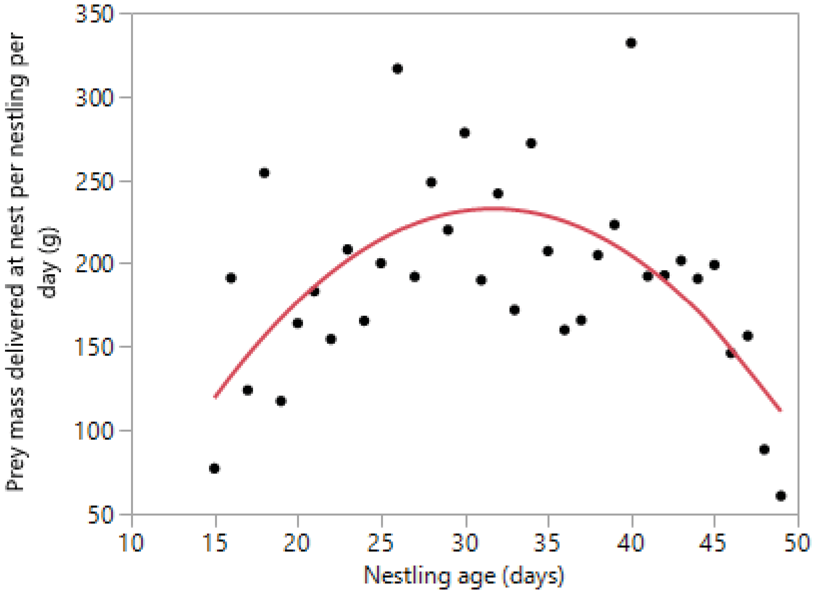

Figure 3: Prey mass delivered at the two marsh harrier nests per nestling per day, as a response of nestling age (n = 35).
Mass/nestling/day = – 175.6 + 25.8*Nestling age – 0.41*(Nestling age)^2

Who captured the prey?

The sex of the parent having captured the prey was determined for 894 of the 921 identified prey items (see methods for definitions). The males had captured 584 (63.5 %) of the prey items recorded, while the females had captured 310. Prey body mass, nestling age, and the interaction between prey class and nestling age significantly affected the probability that the female rather than the male had captured the prey item delivered (table 8). The average gross body mass of prey captured by the female was 86.9 ± 8.2 g, whereas the average gross body mass of prey captured by the male was 54.8 ± 3.5 g.

Table 8: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a female marsh harrier had captured the prey item delivered at the nest (n = 885).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	-0.161	0.301	0.29	0.592
Gross prey mass	0.002	0.001	10.30	0.001
Nestling age	-0.019	0.009	4.95	0.026
Class Aves vs Mammalia	-0.262	0.075	12.14	<0.001
Class Aves vs Mammalia*Nestling age	-0.032	0.009	12.75	<0.001

There was a difference between the male and the female in distribution of class of prey captured (Appendix 2). The male captured more avian prey than expected and the female captured more mammalian prey than expected ($\chi^2 = 14.463$, df = 1, p = <0.001). Also within the avian prey there were differences ($\chi^2 = 25.777$, df = 5, p = <0.001). Of the avian prey, the female captured 13 out of the 15 ducks. Out of the prey captured by the female, water voles amounted for 31.5 %, while 21.1 % of the prey captured by the male was water voles.

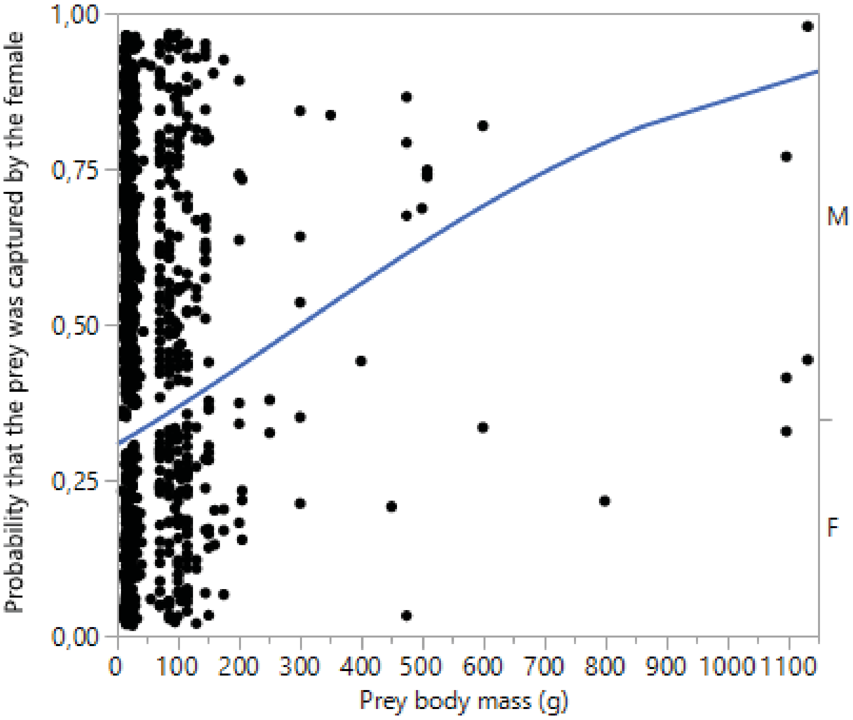

Figure 4: The probability that a marsh harrier female (F) rather than a male (M) had captured prey item as a function of the prey body mass (n = 885)

Who delivered the prey?

The sex of the parent delivering the prey item was determined for 898 of the 921 identified prey items delivered at the nests. The male delivered 502 (55.9 %) of the recorded prey items, while the female delivered 396 (44.1 %). There was a significant effect of nestling age, prey body mass, prey class, and the interaction between prey class and nestling age, on the probability that a prey item was delivered at the nest by the female (table 9). The probability that the female delivered a prey at the nest increased with increasing prey body mass and decreased with increasing nestling age for both avian and mammalian prey, but the decrease was faster for avian prey (figure 5). In total, the female delivered 24,630 g prey biomass at the nests, while the male delivered 22,471 g.

Table 9: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a female delivered a prey at the marsh harrier nest (n = 889).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	2.393	0.329	52.62	<0.001
Gross prey mass	0.006	0.001	16.22	<0.001
Nestling age	-0.093	0.010	87.14	<0.001
Class Aves vs Mammalia	-0.168	0.080	4.42	0.036
Class Aves vs Mammalia*Nestling age	-0.055	0.009	30.49	<0.001

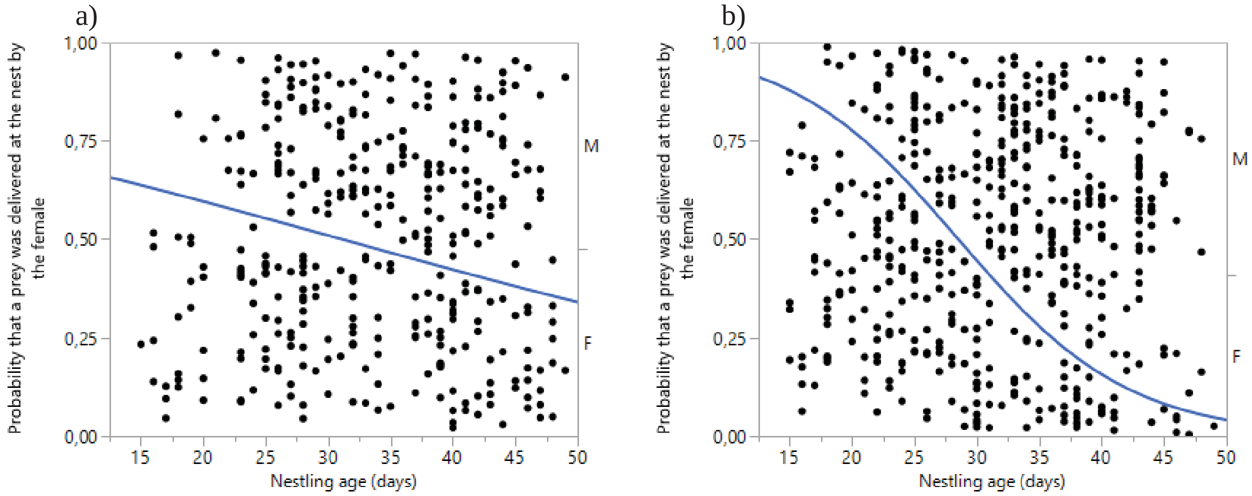

Figure 5: The probability that the marsh harrier female (F) rather than the male (M) delivered a) a mammalian prey (n = 389) and b) an avian prey (n = 500) at the nest as a function of nestling age, for two nests of marsh harriers in Norway.

Of the 584 prey items that were captured by the male 82 were transferred to the female outside the nest and delivered at the nest by the female. The probability that the prey item caught by the male was transferred to the female before delivering was significantly affected by the age of the nestlings and marginally non-significantly affected by prey class (table 10). The probability that a prey item captured by the male was transferred to the female before delivering decreased with increasing nestling age (figure 6), and was marginally higher for a bird, than a mammal.

Table 10: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a prey item captured by a marsh harrier male was transferred to the female before being delivered at the nest (n = 578).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	7.803	0.906	74.24	<0.001
Nestling age	-0.358	0.037	94.70	<0.001
Class Aves vs Mammalia	0.328	0.183	3.21	0.073

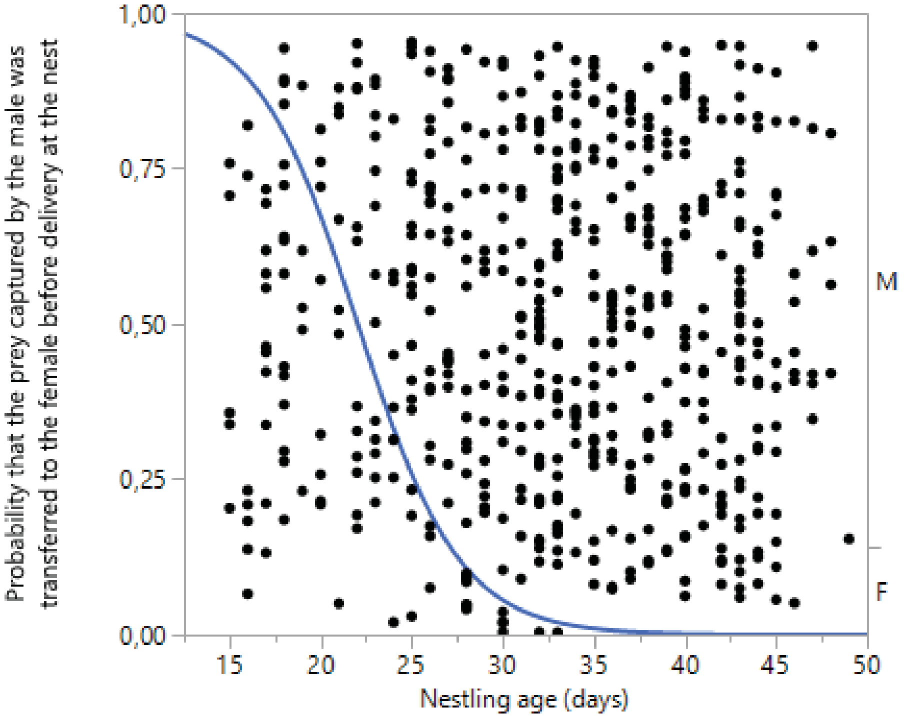

Figure 6: The probability that a prey item captured by a marsh harrier male had been transferred to the female before being delivered at the nest (F), rather than the male delivering the prey item directly at the nest (M), as a function of nestling age (n = 578).

The females delivered a total of 388 prey items at the nests during the monitoring period. Of these, 82 had been captured by males and transferred to the females outside the nest. The probability that a prey item delivered at the nest by the females had been captured by the female was significantly affected by the age of the nestling (table 11). The probability that a prey item delivered at the nest by the female had been captured by the female increased with increasing age of the nestlings (figure 7).

Table 11: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a prey item delivered at marsh harrier nests by the female had been captured by the female (n = 375).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	-5.176	0.748	47.92	<0.001
Nestling age	0.254	0.032	64.17	<0.001

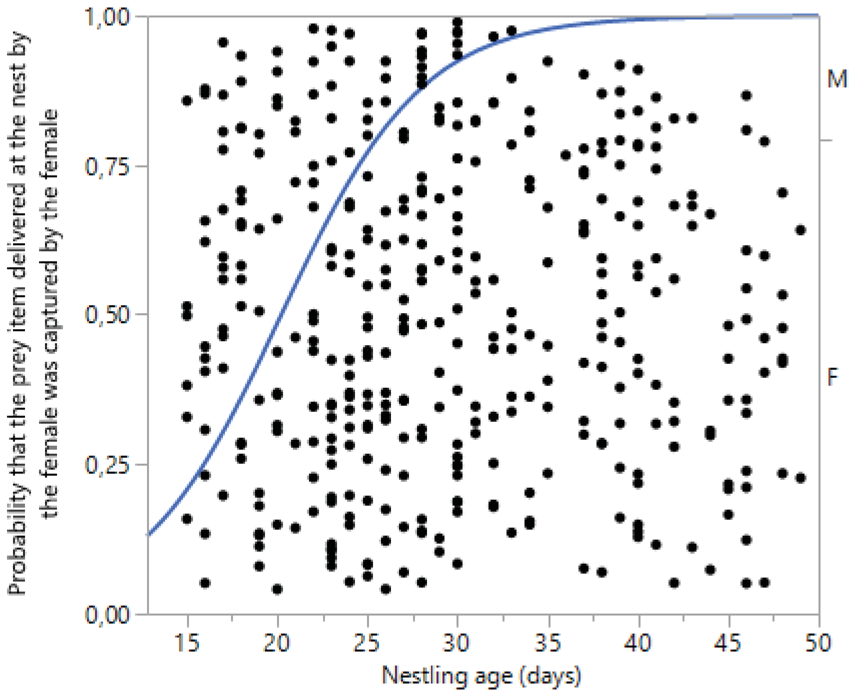

Figure 7: The probability that a prey item delivered at marsh harrier nests by the female was captured by the female (F) rather than the male (M) as a function of nestling age (n = 375).

Preparation outside the nest

Out of 897 prey items that were possible to examine, 145 (16.4 %) were decapitated before being delivered at the nest. Of the decapitated prey items, 126 (86.9 %) were mammals and 19 (13.1 %) were birds. There was a significant effect of prey body mass on the probability that a prey item was decapitated prior to delivery at the nest, and this effect differed between the avian and mammalian prey. The interactions between prey mass and nestling age, prey mass and the sex of the parent capturing the prey, the age of the nestlings and the sex of the parent capturing the prey, and prey mass and prey class were also significant (table 12). The effect of the parent that delivered the prey item was not significant ($\chi^2 = 0.013$, p = 0.909); of the prey items captured by males, 13.6 % of those delivered by the females at nests were decapitated, while 13.2 % of those delivered by males were decapitated.

Table 12: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a prey item delivered at a marsh harrier nest was decapitated prior to delivery (n = 864).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	-3.996	0.690	33.52	<0.001
Prey mass	0.026	0.003	79.29	<0.001
Nestling age	-0.010	0.019	0.27	0.603
Capturing parent (female vs male)	0.307	0.161	3.63	0.057
Class Aves vs Mammalia	-1.134	0.219	26.67	<0.001
Prey mass*Nestling age	-0.001	0.000	5.48	0.019
Prey mass*Capturing parent (female vs male)	-0.008	0.003	6.83	0.009
Nestling age*Capturing parent (female vs male)	0.055	0.017	10.41	0.001
Class Aves vs Mammalia*Prey mass	-0.007	0.002	8.21	0.004

The probability of decapitation prior to delivery at the nest increased with increasing age of the nestlings, and it was more likely that a mammal, rather than a bird, was decapitated. Of the mammals, 33.2 % was decapitated, while 3.7 % of the birds were recorded as decapitated. The probability of decapitation increased with nestling age, but the effect depended on prey body mass, the probability increased faster for large prey than for small prey (figure 8). The probability of decapitation prior to delivery at the nest increased with increasing prey mass both for prey item captured by males and for those captured by females, but the male decapitated smaller prey than did the female (figure 9). The probability of decapitation prior to delivery increased with increasing prey mass for both mammals and birds, but the effect differed between them; the probability of decapitation increased faster with prey mass for mammals than for birds (figure 10).

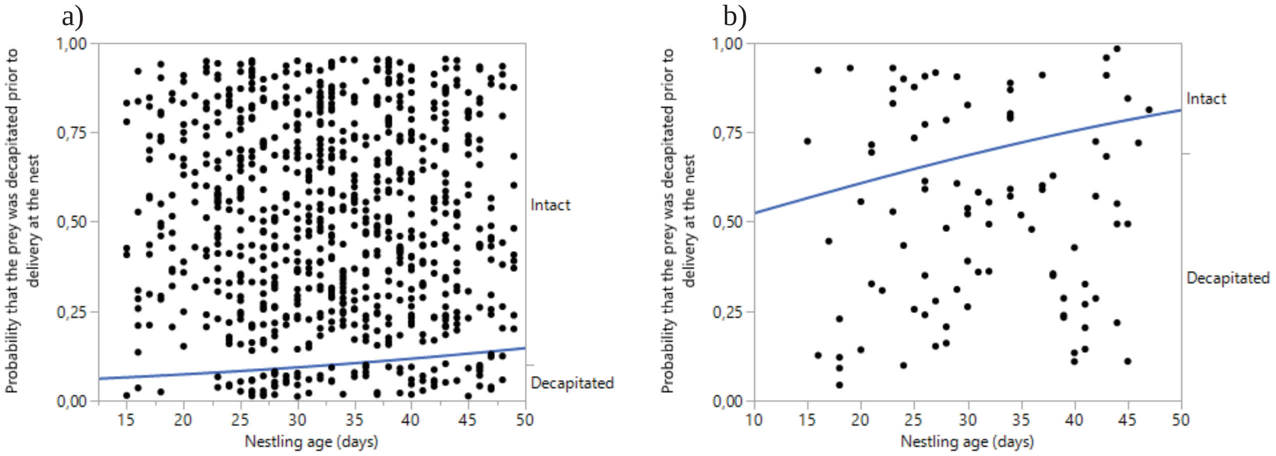

Figure 8: The probability that a prey item delivered at a marsh harrier nest was decapitated prior to delivery as a function of age of the nestlings for a) prey <125 g (n = 772) and b) prey ≥125 g (n = 92). The median of the 145 decapitated prey items was 125, and was therefore chosen as the separating value.

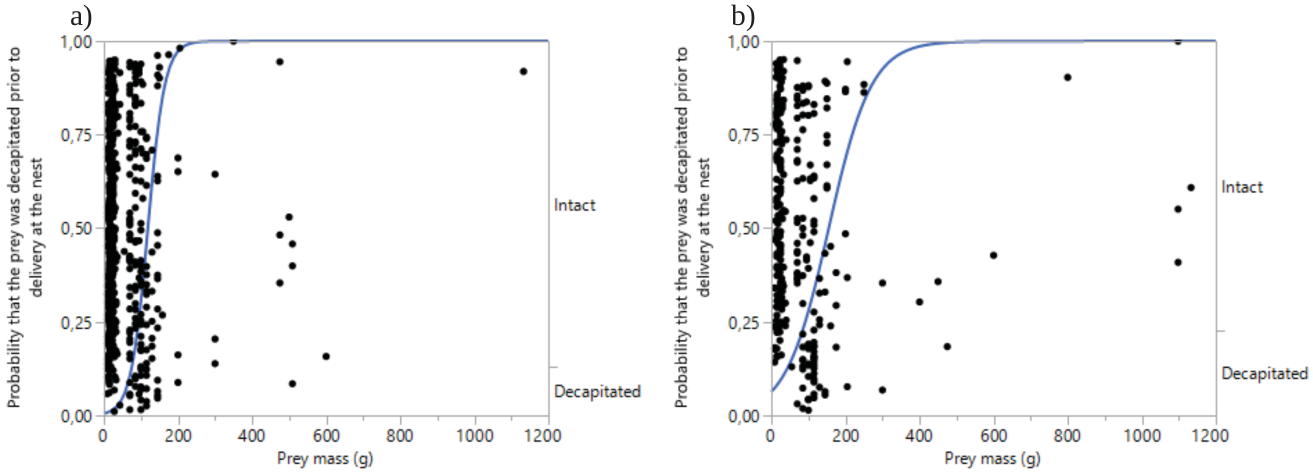

Figure 9: The probability that a prey item delivered at a marsh harrier nest was decapitated prior to delivery as a function of prey body mass. a) Prey items captured by the male marsh harrier (n = 569). b) Prey items captured by the female marsh harrier (n = 295).

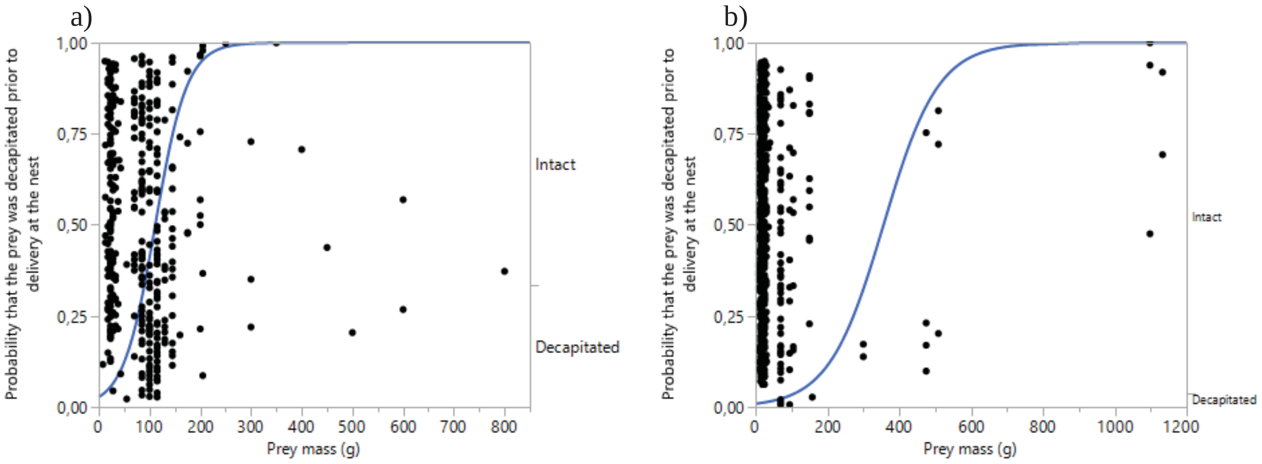

Figure 10: The probability that a prey item delivered at a marsh harrier nest was decapitated prior to delivery as a function of prey body mass for a) mammalian prey (n = 378) and b) avian prey (n = 509).

For mammalian prey separately, the effect of prey body mass was significant on the probability that a mammalian prey was decapitated before being delivered at the nest. The probability that a mammalian prey item was decapitated prior to delivery at nest increased with prey body mass and decreased with nestling age, but the effect of nestling age differed between items captured by the male and items captured by the female (table 13). For the former, the probability of decapitation decreased with nestling age (figure 11a), while for the latter the probability of decapitation increased with nestling age (figure 11b)

Table 13: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that a mammalian prey item delivered at a marsh harrier nest was decapitated prior to delivery (n = 366).

Term	Estimate	SE	χ^2	p
Intercept	-2.934	0.669	19.23	<0.001
Prey mass	0.032	0.004	68.74	<0.001
Nestling age	-0.019	0.018	1.14	0.285
Capturing parent (female vs male)	0.214	0.145	2.19	0.139
Capturing parent (female vs male)*Nestling age	0.049	0.018	7.66	0.006

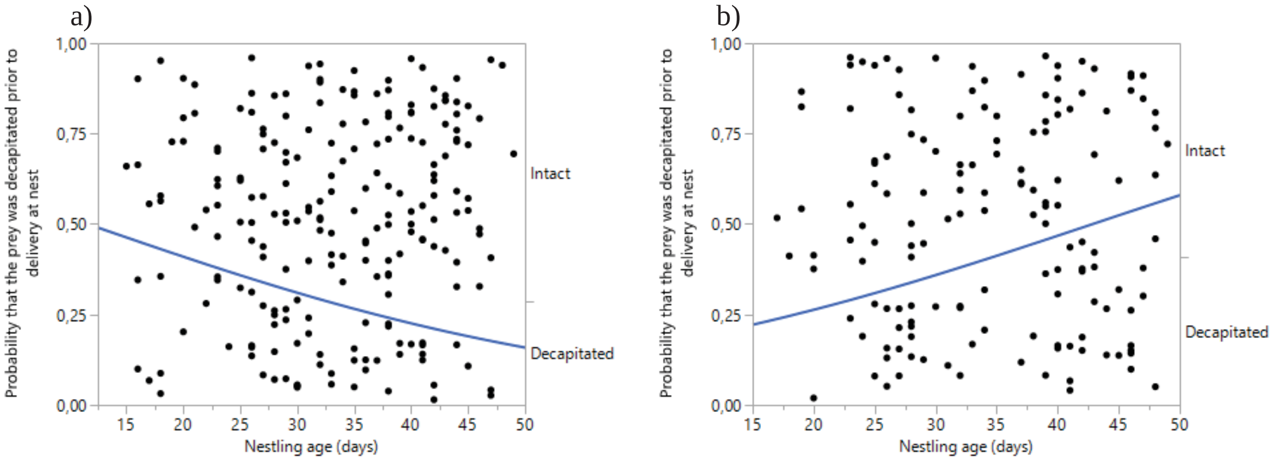

Figure 11: The probability that a mammalian prey delivered at a marsh harrier nest was decapitated prior to delivery as a function of nestling age. a) Prey items captured by the male marsh harrier (n = 217). b) Prey items captured by the female marsh harrier (n = 149).

The probability that an avian prey item was decapitated before being delivered at the nest was significantly affected by the body mass of the prey, but the effect of prey body mass depended on the age of the nestlings (table 14). At all ages, the probability of decapitation increased with increasing prey body mass, but the increase was faster when the nestlings were younger. The probability of decapitation was higher if the female had captured prey rather than the male. However, if one mallard that was delivered with its head intact, but a large proportion of its body removed is excluded from the data, the probability of decapitation prior to delivery was affected by the body mass of the avian prey only ($\chi^2 = 15.79$, $p < 0.001$).

Table 14: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that an avian prey item delivered at a marsh harrier nest was not decapitated prior to delivery at the nest (n = 498).

Term	Estimate	SE	χ^2	p
Intercept	-7.954	2.444	10.59	0.001
Prey mass	0.034	0.009	14.77	<0.001
Nestling age	0.017	0.050	0.09	0.770
Capturing parent (female vs male)	-1.680	0.838	4.02	0.045
Prey mass*Nestling age	-0.002	0.001	11.00	<0.001

Feeder

Of the 945 prey items ingested at the nests, the nestlings ingested 649 (68.7 %) unassisted. The net prey body mass, the age of the nestlings, and the interaction between prey class and net prey mass significantly affected the probability that the female fed the nestlings rather than the nestlings ingested prey unassisted (table 15). The effect of net prey body mass on the probability that the female fed the nestlings differed between avian and mammalian prey. For both prey types, the probability that the female fed the nestlings increased with net prey body mass, but the increase was faster for mammalian prey than for avian prey (figure 12). The probability that the female fed the nestlings decreased with increasing nestling age (figure 13). The nestlings become more likely to ingest the prey unassisted than to be fed by the female when they were older than 27.6 days of age.

Table 15: Parameter estimates from a likelihood ratio test in a logistic regression model of the probability that the marsh harrier female fed the nestlings, rather than the nestlings ingested the prey unassisted (n = 907).

Explanatory variable	Estimate	SE	χ^2	p
Intercept	8.584	0.651	173.85	<0.001
Prey net mass	0.014	0.002	37.78	<0.001
Nestling age	-0.342	0.024	208.37	<0.001
Class Aves vs Mammalia	0.206	0.115	3.16	0.076
Class Aves vs Mammalia*Prey net mass	-0.006	0.002	7.11	0.008

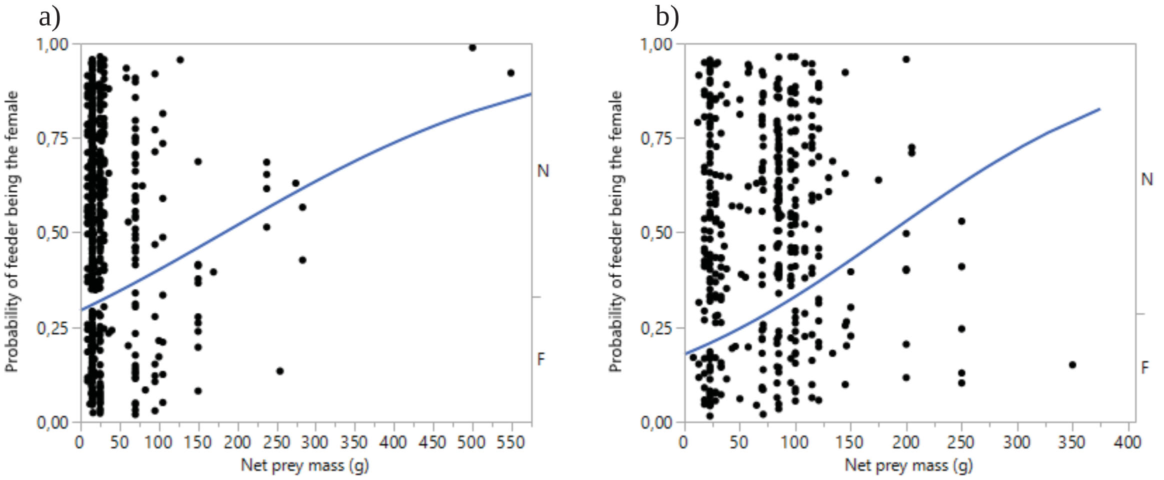

Figure 12: The probability that the female fed the nestlings (F) rather than the nestlings ingested prey unassisted (N), as a function of net prey body mass for a) avian prey (n = 509) and b) mammalian prey (n = 396).

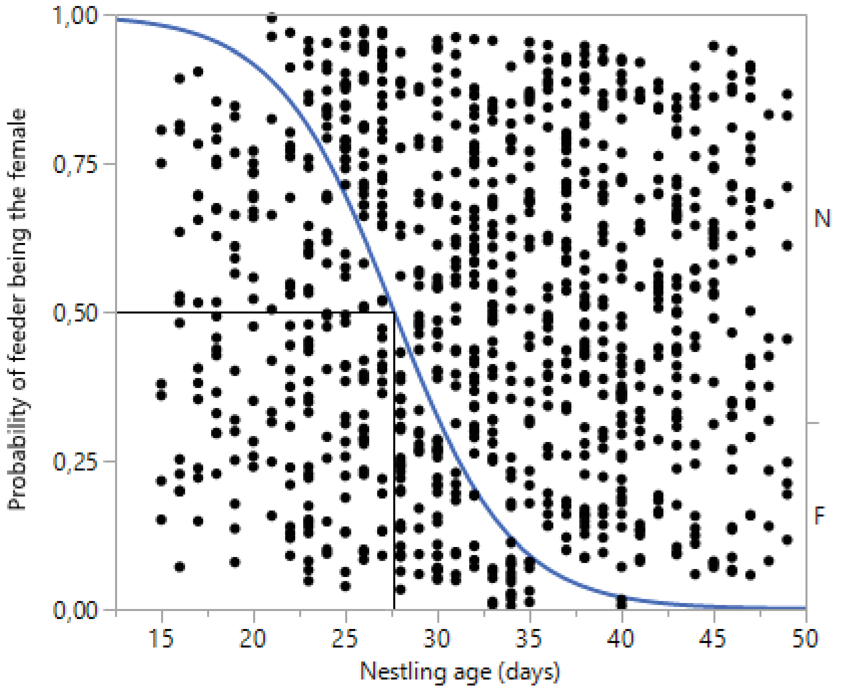

Figure 13: The probability that the marsh harrier female fed the nestlings (F) rather than the nestlings ate unassisted (N) as a function of the age of the nestlings (n = 945).

Feeding time when the female fed the nestlings

Handling time was calculated for the 242 prey items handled by the female. Prey class, net prey mass ($\log_{10}$-transformed), nestling age, and the interaction between prey class and net prey mass, significantly affected the handling time ($\log_{10}$-transformed) when the female fed the nestlings (table 16). In general, handling time was longer for an avian prey than for a mammalian prey with the same body mass. For both prey types the handling time increased with increasing net prey mass, but the increase was significantly faster for mammalian prey than for avian prey (table 16, figure 14). The handling time decreased with increasing age of the nestlings. The ingestion rate, defined as mass ingested per feeding time, increased with increasing prey mass for both avian and mammalian prey (figure 17a), however the slope was larger than zero only for avian prey (slope = 0.0018 ± 0.00058), not for mammalian prey (slope = 0.0011 ± 0.00088).

Table 16: Parameter estimates from a generalized linear model (GLM) of significant effects on handling time ($\log_{10}$-transformed) for prey items delivered at two marsh harrier nests when the female fed the nestlings (n = 233).

Explanatory variable	Estimate	SE	t	p
Intercept	1.350	0.149	9.09	<0.001
Net prey mass ($\log_{10}$)	0.773	0.067	11.54	<0.001
Nestling age	-0.021	0.004	-4.81	<0.001
Class Aves vs Mammalia	0.056	0.027	2.05	0.041
Class Aves vs Mammalia * Net prey mass ($\log_{10}$)	-0.159	0.067	-2.38	0.018

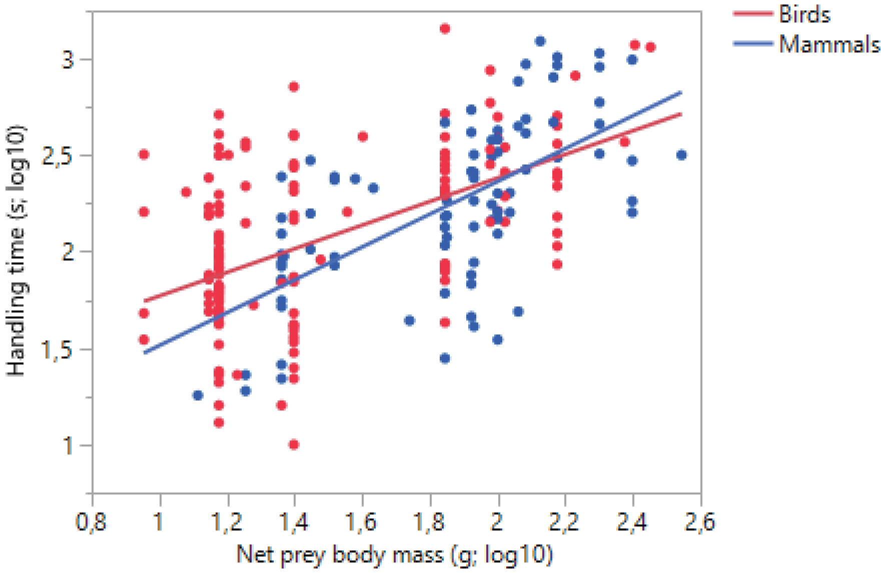

Figure 14: Handling time ($\log_{10}$-transformed) as a function of net prey body mass ($\log_{10}$-transformed) when the marsh harrier females fed the nestlings, for avian and mammalian prey separately (n = 233).

Feeding time when the nestlings fed unassisted

Handling time was calculated for 121 of the prey items handled by the nestlings unassisted. When the nestlings ingested prey unassisted the handling time ($\log_{10}$-transformed) was significantly affected by net prey body mass ($\log_{10}$-transformed), by whether the prey was a rodent or a passerine, and the interaction between net prey body mass and whether the prey was a rodent or a passerine (table 17). In general, handling time was longer for avian prey than for mammalian prey with the same body mass. For both prey types the handling time increased with increasing net prey body mass, but the increase was significantly faster for rodents than for passerines (table 17, figure 15). The age of the nestling had no significant effect (t = -1.05, df = 4, p = 0.298). The handling time when the nestlings handled prey unassisted was in general longer than when the female fed the nestlings (table 18, figure 16a).

Table 17: Generalized linear model (GLM) of significant effects on handling time ($\log_{10}$-transformed) for prey items delivered at two marsh harrier nests when the nestlings ingested prey unassisted (n = 121).

Explanatory variable	Estimate	SE	t	p
Intercept	1.339	0.169	7.90	<0.001
Net prey mass ($\log_{10}$)	0.707	0.111	6.35	<0.001
Prey order Passerine vs Rodentia	0.108	0.036	2.96	0.004
Prey order Passerine vs Rodentia *Net prey mass ($\log_{10}$)	-0.253	0.111	-2.28	0.025

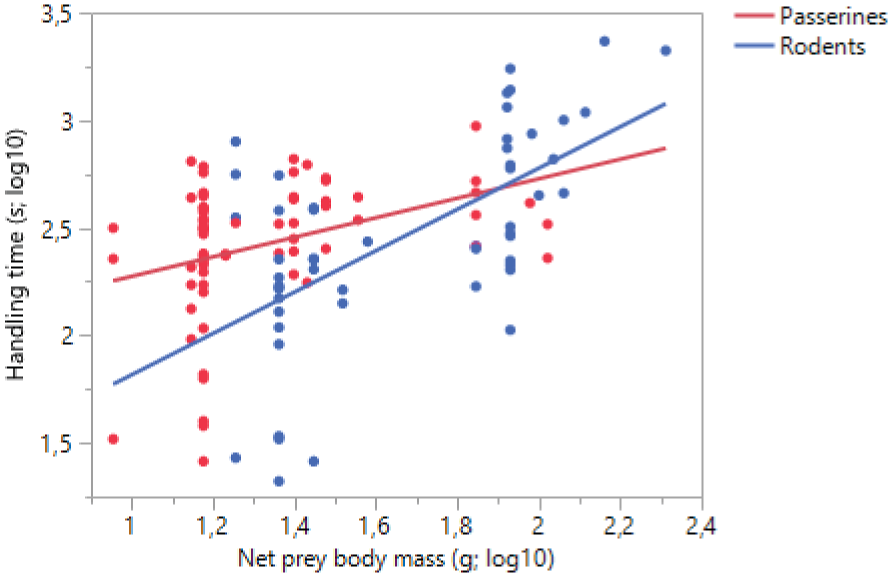

Figure 15: Handling time ($\log_{10}$-transformed) as a function of net prey body mass ($\log_{10}$-transformed) when the marsh harrier nestlings ingested prey unassisted, rather than being fed by the female, for passerine and rodent prey separately (n = 121).

Tabell 18: Generalized linear model (GLM) of significant effects on handling time for prey delivered at two marsh harrier nests (n = 357).

Explanatory variable	Estimate	SE	t	p
Intercept	97.626	19.575	4.99	<0.001
Net prey mass	4.510	0.323	13.96	<0.001
Handler (female vs nestling)	-146.409	14.103	-10.38	<0.001
Handler (female vs nestling)*Net prey mass	-2.101	0.323	-6.50	<0.001

In general, the ingestion rate increased slightly with increasing prey mass when the nestlings fed unassisted (figure 16b). However, the increase was not significantly different from zero (slope = 0.000778 ± 0.000485). The ingestion rate was lower when the nestlings ingested unassisted than when the female fed the nestlings (figure 16b). The ingestion rate when the nestlings ingested unassisted increased with prey body mass for avian prey, but decreased with prey body mass for mammalian prey (figure 17b), but the latter was not significantly different from zero (slope = -0.000853 ± 0.000823).

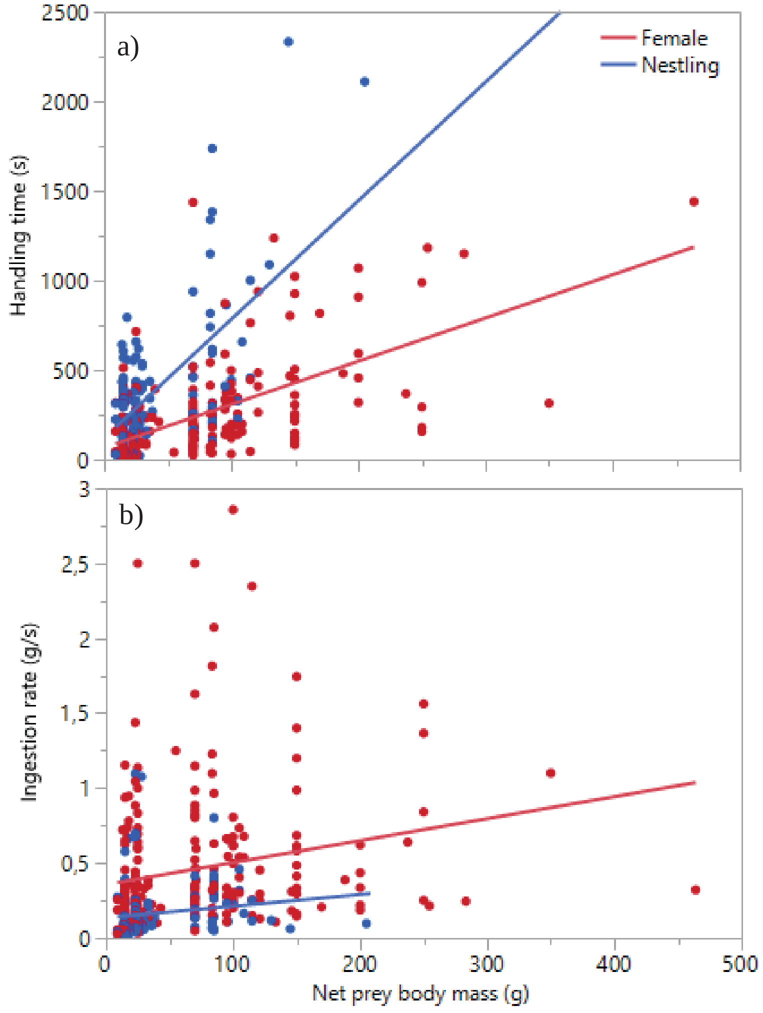

Figure 16: Handling time (a) and ingestion rate (b) as a function of net prey body mass when the marsh harrier female fed the nestlings (n = 233) and when the nestlings ingested prey unassisted (n = 121).

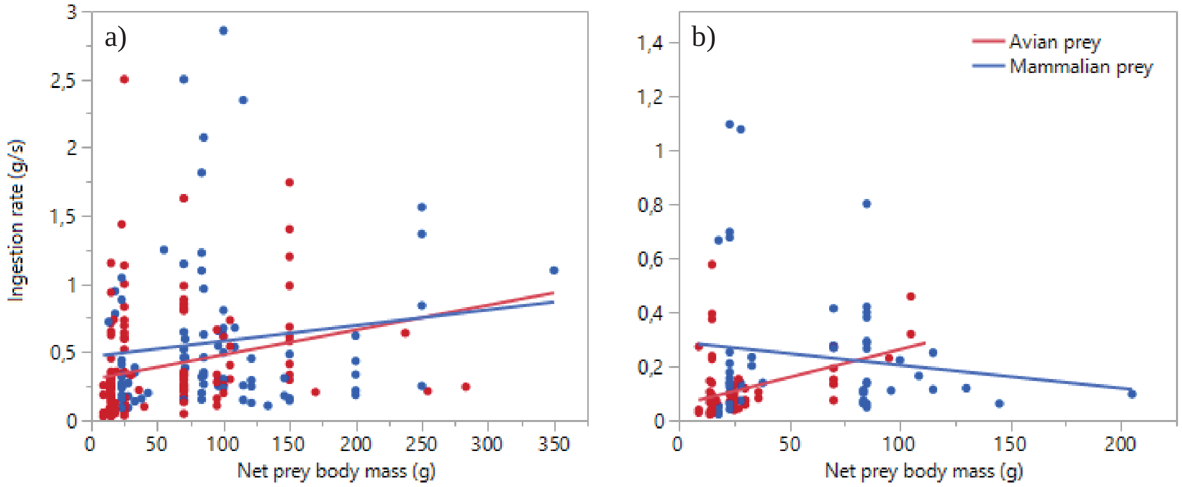

Figure 17: Ingestion rate as a function of net prey body mass when a) the female marsh harrier fed the nestlings (n = 233) and b) the nestlings ingested prey unassisted (n = 121).

Discussion

Diet composition

Of the 921 identified prey items recorded as delivered at the two marsh harrier nests, 55.4 % were birds, 43.4 % were mammals, and the remaining 1.2 % were amphibians, fish and reptiles. Other studies of marsh harrier diet have shown a great variety of prey, some studies found mammals to be the most contributing prey by number (Brzeziñski & Żmihorski 2009), while most studies found that avian prey was dominating (Bock 1978, Witkowski 1989, Tornberg & Haapala 2013). The composition of the diet of marsh harriers has been found to differ between nests (Brzeziñski & Żmihorski 2009, Cardador et al. 2012) and between years in the same area (Bock 1978). Common trend is that the diet of marsh harriers consists of a high number of species, especially avian species (Bock 1978, Witkowski 1989, Tornberg & Haapala 2013).

In my study, mammals contributed with 60.3 % of the total biomass delivered at the two nests during the monitoring period, of which water voles contributed 24.5 % by number and 45.0 % of the total biomass. Avian prey accounted for 38.0 % of the total biomass, and passerines contributed with 73.7 % of the avian biomass and 28.0 % of the total biomass. Both Brzeziñski & Żmihorski (2009) and Tornberg & Happala (2013) found that waterfowl accounted for 60-70 % of the biomass delivered during the nestling period, which markedly contrast with my study, where waterfowl only accounted for 6.9 % for the total biomass.

The main differences between my results and those from earlier studies is the high percentage of mammalian prey, the high percentage of biomass contributed by passerines, and the low numbers of waterfowl. Brzeziñski & Żmihorski (2009) found high numbers of mammalian prey (73.1 %), mainly *Microtus* voles, but the biomass of mammalian prey only accounted for 23.2 %, compared to 60.3 % overall in my study and 67.8 % at the nest at Hellesjøvannet. Brzeziñski & Żmihorski (2009) found that waterfowl and domestic chicken accounted for 71.0 % of the biomass consumed. Non-passerine birds has been found to be the most important prey group also in other studies of the marsh harrier (Underhill-Day 1985, Witkowski 1989, Tornberg & Haapala 2013), while they in my study, however, only accounted for 10.0 % of the total biomass. Passerines accounted for 95.3 % of all avian prey and 51.3 % of total prey in my study, and contributed with 28 % of the total biomass. Passerines were common prey in several studies, accounting for 50-60 % of total number of prey (Bock 1978, Tornberg & Happala 2013), which corresponds with my results, but the high contribution by passerines of total biomass is rare.

The lack of waterfowl as prey in my study may have several reasons. At Rokkevannet, I did not observe any breeding waterfowl in 2016, possibly making it more beneficial for the marsh harriers to hunt other prey. In Akershus, where Hellesjøvannet is located, there were high numbers of water vole in 2016 (V. Selås, pers.comm.). Even with breeding colonies of ducks and grebes (Podicipedidae) at the lake, the high numbers of water voles could explain why there was a lack of waterfowl in the diet at Hellesjøvannet, as other generalist predators also show a functional response to rodents (Selås 2001). The water vole accounted for 40.8 % of the prey by number and 62.6 % by biomass at Hellesjøvannet. The diet of the generalist marsh harrier seems to reflect the local fauna in composition. The muskrat (*Ondatra zibethicus*) was an important prey in Finland (Tornberg & Haapala 2013), and Underhill-Day (1985) found that pheasant and lagomorphs were important in Great Britain. Lagomorphs accounted for 14.5 % of the biomass consumed at the nest at Rokkevannet in my study.

Sexual difference in prey selection

The female marsh harriers captured heavier prey than the males, as well as more mammals relative to avian prey, while the male captured more avian prey relative to mammals. It is a well known fact that female raptors are capable of capturing heavier prey than their male counterparts (Newton 1979, Cramp & Simmons 1980), and Witkowski (1989) found the same difference for the marsh harrier, which was also supported by Tornberg & Haapala (2013). This pattern has also been found in other harrier (*Circus*) species (Balfour & Macdonald 1970, Schipper 1973, Picozzi 1978). The larger body size of females make large prey more accessible for them. Witkowski (1989), who found that during the incubation period, 63 % of the prey delivered by the male to the female were common voles (*Microtus arvalis*), supports this hypothesis. The proportion of common voles did not change after hatching of the nestlings, and the increasing number of large prey delivered to the nestlings started as the female joined the male in hunting efforts (Witkowski 1989). In Finland, passerines were the dominating prey group in the early nestling period, whereas the importance of mammals and larger non-passerine birds increased in the later parts of the breeding season (Tornberg & Haapala 2013), also supporting that the female may capture larger prey. The load size effect may be a factor influencing the size of prey. Small prey items should, in terms of energy, not be worth transporting over long distances (Sonerud 1992). This could be applicable for marsh harrier males, which uses larger home ranges (Cardador et al. 2009), and often hunt far from the nest (Cramp & Simmons 1980). If he hunts farther from the nest than the female do, he should hunt heavier prey, however, in periods with a high demand after prey, the male may bring all captured prey back to the nest, regardless of size and distance from nest. The male prey unselectively on all prey, while the female may prey selectively on large prey.

The adult marsh harriers differed in thir prey selection in my study. The female captured proportionally more mammals than the male, in particular water voles. Concerning avian prey, the female captured proportionally five times more non-passerines than the male, whose avian prey consisted of 97.8 % passerines. This result seems consistent to what Tornberg & Haapala (2013) found in Finland, and that the diet of marsh harriers in Poland changed from mainly voles to also including nestlings of waterfowl as the female joined the male hunting (Witkowski 1989). Schipper (1973) found that males hunted more passerines than did females, and that water birds were captured mainly by the female, corresponding to my results. On the other hand, Brzezinski & Zmihorski (2009) failed to find a difference in prey selection between the male and the female.

Observations made by Witkowski (1979) illustrate that male and female marsh harriers hunt in different habitats, the male hunts mainly in terrestrial habitats, while the female hunts in aquatic habitats. This may explain why the diet in the early nestling periods consisted of small terrestrial animals, including more aquatic and semi-aquatic prey, such as fish, waterfowl and frogs, when the female starts hunting (Schipper 1973, Witkowski 1989). A reason for the habitat separation might be that the male utilize a larger home range than the female in the breeding season (Cardador et al. 2009), making him encounter terrestrial habitats more often than the female, whose home range mainly surrounds the nest in wetlands (Tornberg & Haapala 2013). This seems consistent with the females in my study mainly capturing waterfowl and aquatic water voles, and also fish.

A comparison of male and female prey selection based on observations of prey items delivered at the nest may be biased due to the prey transfers from the male to the female outside the nest (Sonerud et al. 2013), a common phenomenon in harriers (Witkowski 1979, Cramp & Simmons 1980, Wiącek 2006). Fernández & Azkona (1994) found that nearly 60 % of all prey captured by the male were transferred to the female outside the nest. This fact makes it difficult to record which sex captured the prey being delivered at the nest by the female. Fernández & Azkona (1994) and Kitowski (2006) found that the female hunts approximately 20 % of the total prey number, compared to nearly 40 % in my study. We must therefore take into account that some of the prey recorded as captured by the female in fact was captured by the male. This fact is probably also the reason why my model showed that the male contributed with more prey as the nestlings became older, as earlier studies show that the male hunts nearly all prey during the incubation and early nestling periods (Schipper 1973, Witkowski 1989, Kitowski 2006). The difference in prey selection between the male and the female could therefore in fact be even larger than show in this study.

Daily and seasonal patterns of prey deliveries

The probability that a mammalian prey, rather than an avian prey, was delivered at the nest increased as the nestlings become older, consistent with findings by Underhill-Day (1985). This could be because the nestlings sooner became able to handle small mammals themselves as they have less protruding parts (Sonerud et al. 2014b). However, the season might be more important than the age of the nestlings. Other studies have shown that most of the avian prey in the marsh harrier diet are juvenile birds (Hildén & Kalinainen 1966, Underhill-Day 1985). Whether passerines were adult or juveniles were not classified in my study, but some of the passerines were identified as juveniles. A possible reason why relative fewer avian prey were delivered as the nestlings become older could be the decreasing availability of juvenile birds as the season progressed rather than the marsh harrier nestling age. Juvenile birds are vulnerable and more available early in the season as they just have left the nest, and become more difficult to capture as they develop during the season (Sullivan 1989, Magrath 1991).

The distribution pattern between avian and mammalian prey did not just reveal seasonal patterns, but also daily patterns. The time of overall deliveries show a monophasic pattern with a relatively even probability of prey delivery from 08.00 to 20.00 hours, with rising probability from 05.00 to 08.00 and descending probability from 20.00 to 22.00 hours. This pattern has also been found for other generalist raptors, like the common buzzard (*Buteo buteo*) and the Eurasian kestrel (Reif & Tornberg 2006, Steen et al. 2011). The probability for delivery of an avian prey was highest between 16.00 and 19.00 hours. Reif & Tornberg (2006) found that prey deliveries at nests of the northern goshawk (*Accipiter gentilis*), with a diet mainly consisting of avian prey (Widén 1987, Sonerud et al. 2014a), peaked in the morning and the afternoon, a pattern also found in peregrine falcon (*Falco peregrinus;* Jenkins 2000, Bech 2016). These are the periods where passerines are most active and thus easiest to detect and capture (Thirgood 1995, Trnka 2006). I found no peak in probability of prey delivered being a bird in the morning hours. However, the probability of the prey delivered being a mammal peaked in the morning, and thus giving an even probability of prey delivery throughout the whole activity period of the marsh harrier.

The daily delivery rate, measured in prey mass per day, was affected by the age of the nestlings. The prey mass delivered at the nest increased up to an age of 31.5 days, and thereafter decreased rapidly. It is likely that the parents of raptors adjust their feeding effort to the demand of the nestlings (Steen et al. 2012). I would expect that the daily prey mass delivered at the nest would increase until the start of the fledging period because as the nestlings are growing they need more energy, as well as increased activity level. By the start of the fledging period the nestlings are also provided prey outside the nest, and the delivered prey mass at the nest will decrease. Krijgsveld et al. (1998) found that the maximum food intake by hand raised marsh harriers occurred at the age of 22-24 days, considerably later than the maximum growth rate at 12-15 days, but still earlier than found in my study. Marsh harrier nestlings reach their maximum body mass after approximately 35 days (Krijgsveld et al. 1998), some days after the maximum prey mass delivery that I found. This is approximately the age at which the nestlings start to fledge (Cramp & Simmons 1980, Krijgsveld et al. 1998), and some days before I observed the first flying nestling, at an age of 40 days at Rokkevannet. However, I did not measure neither the growth rate nor food intake, but the results shows that the parents provided increasing prey mass to the nest until the fledging period, whereas the nestlings were also provided prey outside the nest.

Which parent delivered the prey?

Of the prey items delivered at the marsh harrier nest in my study, the male delivered more than half (55.9 %), and the proportion prey delivered by the male increased during the nestling period. This proportion is a remarkably high and more than twice as high as found in other studies (Fernández & Azkona 1994, Kitowski 2006, Brzeziñski & Żmihorski 2009). The reason for this high number is probably that I started recording when the nestlings were 15 and 22 days of age, respectively. In the 37 days of early nestling period that I missed, the male probably transferred nearly all prey items to the female outside the nest (Schipper 1973, Witkowski 1989, Kitowski 2006). The increasing proportion delivered by the male is as expected, as the female allows the male to deliver prey directly at the nest as the nestlings became older (Sonerud et al. 2013) and the nestlings become able to ingest by themselves (Cramp & Simmons 1980).

The asymmetric parental role differentiation in the marsh harrier and other raptors suggests that the male hunts and provide the family with prey, while the female perform feeding and brooding at the nest (Newton 1979, Cramp & Simmons 1980). As expected, the female performed all the feeding and brooding at the nest, seen on video, and I observed aerial prey transfers from the male to the female outside the nest 25 times. The male captured the majority of the prey, either delivered directly or transferred to the female (Cramp & Simmons 1980, Sonerud et al. 2013). The distinct roles of raptors during the breeding season is linked to the evolution of reversed size dimorphism (RSD), which is well documented and exists in various degree in nearly all raptor species (Newton 1979). A high degree of RSD is regarded as an adaptation to differentiate the niches of the sexes to avoid competition in the breeding season, and an adaptation for the males to hunt agile avian prey (Newton 1979, Andersson & Norberg 1981).

Sonerud et al. (2014a) found that the degree of RSD, calculated as the ratio between the length of the wing of female and male, was is related to female confinement to the nest for feeding the nestlings, prey size and the proportion of avian prey in the diet. The marsh harrier has a medium degree of RSD, the wing length of the female is 1.05 times the male’s wing length (Cramp & Simmons 1980). With approximately 50 % of avian prey in the diet, and a female confinement, defined as the age of the nestlings where they ingest >50 % of the prey items unassisted, at 27.6 days in my study, it is possible to compare the marsh harrier with other generalist raptors. In terms of proportion of avian prey in the diet, the marsh harrier is located between the eagle owl (*Bubo bubo*) and the golden eagle (*Aquila chrysaetos*), and the female confinement is also located between the eagle owl and the golden eagle, as expected by Sonerud et al. (2014a). However, the RSD for the marsh harrier is smaller than those of the eagle owl and the golden eagle, probably because the marsh harrier hunts smaller prey. The common buzzard hunts smaller prey than the eagle owl and the golden eagle (Reif et al. 2001, Selås et al. 2007), approximately of the same size of the prey of the marsh harrier. With a higher proportion of avian prey in the diet, the female confinement for marsh harriers is twice the confinement for the common buzzard reported by Sonerud et al. (2014a). This could be caused by the similar sized common buzzard’s higher proportion of reptiles in the diet (Selås et al. 2007, Sonerud et al. 2014b) which is easy to ingest. As a result of this, the RSD for common buzzard are marginally smaller than for marsh harriers (Sonerud et al. 2014a). The RSD for marsh harrier fits well in the general pattern of RSD in raptors found by Sonerud et al. (2014a).

Preparation of prey before delivering at nest

My data did not suggest that the female prepared prey items that were captured by the male. Thus, it seems like prepared prey captured by the male was prepared by the male. Of the mammals delivered at the nest, 33.2 % were decapitated prior to delivery, while only 3.7 % of the birds were decapitated. The proportion of decapitated avian prey in my study was remarkably low compared to what have been found in other studies, 60-85 % for peregrine falcon and Eurasian kestrel (Rosenfield et al. 1995, Steen et al. 2010, Bech 2016). This difference could be caused by the relative prey size of the raptors; the feeding constraint hypothesis predicts that small nestlings are unable to swallow large and solid items (Slagsvold & Wiebe 2007). The marsh harrier nestlings are able to ingest the skulls of small passerine prey larger than the Eurasian kestrel nestlings are capable of, and thus have a larger gape size and swallowing capacity, while the passerine prey of the two species is of similar size (Steen et al. 2010, this study). This may reduce the importance of parents reducing the size of small passerine prey by decapitation (Kaspari 1990, Slagsvold & Wiebe 2007). Another possible explanation is that the quality of my video clips was poor, making it difficult to record decapitation for small birds. It was easier to conclude that a bird was not decapitated than that it was decapitated.

For both avian and mammalian prey, the probability of being decapitated increased with increasing body mass. This is consistent with what Steen et al. (2010) found for nesting Eurasian kestrels. Transport of large prey from the capture site to the nest is energy consuming, and by decapitating large prey at the capture site, the predator will reduce the cost of transport and increase the net rate of energy delivery (Sodhi 1992). By partial consumption of large prey, not only are costs of transport reduced, but the energy intake for the parent is also increased (Rands et al. 2000). This reduces the time needed to hunt for self-feeding (Rands et al. 2000). As well as the benefits to the parent, the limitations of the nestlings could explain the decapitation of large prey. By removal of the head of a prey, the proportion of indigestible parts are reduced. Just as prey that are too large to be swallowed should be prepared (Kaspari 1990), parts of prey that are too large to swallow should be removed (Steen et al. 2010). The gap size limits the size of prey and prey parts that are not possible to split in smaller pieces like the skull (Slagsvold & Wiebe 2007, Steen et al. 2010).

Removal of a large head is beneficial, but prey with head not exceeding the gape size should not be decapitated. However, the nestlings' gape size limit and swallowing capacity would increase with age, and the need for decapitation would decrease as the nestlings grow older and larger (Slagsvold & Wiebe 2007), as found by Steen et al. (2010). In my study, the effect of nestling age differed between prey captured by the male and by the female for mammals, but not for birds. The male decapitated prey less frequently as the nestlings became older, while the female decapitated the prey more frequently with increasing nestling age. This indicates that the age of the nestlings is not important, and that partially consuming a prey item before delivering it to the nest reduces the time the parent needs to forage for itself, and thus increases the overall delivery to the nest, as proposed by Rands et al. (2000). I suggest that this is due to the parents' hunting pressure, not the age of the nestlings. When the male hunt for himself, the female and the nestlings, there is a high hunting pressure, and by decapitating prey he reduces the time he needs to forage for himself. However, when the female joins the male in hunting in the later stages of the nesting period, the hunting pressure on the male is reduced, giving him time to hunt for himself and the nestlings, and there would be less need for decapitating prey. As the female join the male in the hunting, she can not longer consume parts of prey delivered by the male at the nest. For her to reduce the time she would need to forage for herself, she would decapitate prey prior to delivery more frequently when the nestlings grow older. Another possible explanation could be that the female captures larger prey than the male and thus the prey's skull would be too large for the nestlings' gape size limit (Steen et al. 2010).

I found that the probability of decapitation increased with prey mass, but the effect of mass depended on other variables as well. The effect of mass differed between mammalian and avian prey, the sex of the capturing parent, and the age of the nestlings. For avian prey, no prey under 70 g was decapitated, and only a handful of prey under 200 g were decapitated. On the other hand, almost all of the decapitated mammalian prey weighed less than 200 g, and the point above which it was more likely that a prey was decapitated was at 100 g for mammalian prey, and approximately 400 g for avian prey. The reason for this pattern could be that removing the head of a bird with a body mass less than 70 g is of little benefit for the parent. The reduce in transportation cost is small (Sodhi 1992), and the head of a small bird is probably not too large for the nestlings to swallow (Steen et al. 2010). The difference between the sexes is may be an effect of the difference in prey size between the sexes. The male captured smaller prey, and it seems like his threshold to decapitate the prey is lower than the female's threshold. When the nestlings became older, the probability for decapitation increased, but the effect was larger for large prey. This does not fit with the fact that the nestlings' gape size limit and swallowing capacity increase with age, so the need for decapitation would decrease (Slagsvold & Wiebe 2007). However, it supports my explanation that the hunting pressure on the parents is more important than the age of the nestlings, and that large prey were decapitated when the nestlings became older due to increasing hunting pressure on the female, forcing her to decapitate prey in order to feed herself.

Feeding at the nest

The probability that the female handled a prey item and fed the nestlings rather than the nestlings ingested the prey unassisted decreased as the nestlings become older, and increased with prey body mass for both mammalian and avian prey. As a nestling grows older, it develop physically until it is able to grip and hold on to a prey with its feet and the bill is able to tear off pieces of meat from the prey. This is common among raptors (Sonerud et al. 2014a). The marsh harrier nestlings handled prey unassisted the first time at 21 days of age in my study, compared to 23-25 days found by Witkowski (1989). From an age of 28 days, they handled more than half of the prey unassisted, even if Witkowski (1989) stated that the nestlings "could not tear the prey well" at about 25 days of age.

The probability that the marsh harrier nestlings ingested a prey item unassisted decreased with increasing prey body mass, as also found for other raptor species by Sonerud et al. (2014a). This effect differed between avian and mammalian prey. The nestlings were more likely to ingest small mammals than small birds unassisted. Avian prey have many protruding parts like bill, wings and long tarsi, possibly making them more difficult to handle, and feeding time of adult raptors has been found to be longer for avian prey than for mammalian prey of same body mass (Slagsvold & Sonerud 2007). This supports that assistance from the female is more needed for smaller avian prey than mammalian prey, and is hypothesized to constrain the female to the nest for feeding the nestlings for a longer time (Sonerud et al. 2013, 2014a). One might think that the effect of nestling age would differ between avian and mammalian prey as well, but no such effect was found in my study. Another explanation may be that by handling and distributing large prey to several nestlings, the female could feed herself as well (Sonerud et al. 2013), and thus reduce time needed to hunt for herself (Rands et al. 2000).

Handling time

For the prey items that the female marsh harrier fed to the nestlings the handling time decreased with increasing age of the nestlings, probably because the nestlings developed physically and because their swallow capacity increased as they grew older. The handling time increased with increasing net prey body mass for both avian and mammalian prey, but the increase was faster for mammalian prey. This is consistent with results from other studies of handling time in raptors (Slagsvold & Sonerud 2007, Sonerud et al. 2014a). The increase in handling time with prey body mass were steeper for mammalian than avian prey, making it more efficient to handle small mammals than small birds, but more efficient to handle large birds than large mammals. For prey with a body mass of less than approximately 120 g, mammals were more efficient to handle, while for prey weighing more than 120 g, birds were more efficient to handle. This may explain why large waterfowls and small mammals often have contributed most to total mass in a marsh harrier diet during the breeding season (Hildén & Kalinainen 1966, Witkowski 1989, Brzeziñski & Żmihorski 2009, Tornberg & Happala 2013). The reason for relatively long handling time for small avian prey may be that it is relatively many indigestible parts like bill and feathers, which require more handling. This applies to avian prey of all sizes, but when a threshold is passed, the ingestion rate can accelerate when the large chunks of meat are reached from avian prey.

The increasing ingestion rate with increasing prey body mass that I found for female feeding the nestlings is opposite of what found for self-feeding raptors (Ille 1991, Slagsvold & Sonerud 2007). One reason for a higher rate when feeding nestlings than when self-feeding may be the fact that morsels from one prey often were given to more than one nestling, so the feeding was less constrained by time spent swallowing (Steen 2010). A second reason may be that the female gave larger pieces to the nestlings than when feeding herself, as partitioning a prey into smaller pieces competes for time needed to hunt and self-feed (Steen 2010). However, this may indicate that it is more efficient to bring large prey items to the nest in the nestling period, contrary to what Slagsvold & Sonerud (2007) suggested.

Also when the nestlings handled prey unassisted the handling time increased with prey body mass, as found for nestlings of Eurasian kestrel (Steen 2010), golden eagle (Skouen 2012) and peregrine falcon (Bech 2016). As when the female fed the nestlings, the handling time increased faster with prey body mass for mammalian prey than for avian prey. The obstacle du to more protruding and indigestible parts in an avian prey than a mammalian prey should be even more relevant when the nestlings have to handle the prey unassisted. The ingestion rate when the nestlings fed unassisted was lower than when the female fed the nestlings, and did not differ for small and large prey, as found for Eurasian kestrel nestling (Steen 2010). This indicates that no prey size is most beneficial to bring to the nestlings, with respect to ingestion rate. On the other hand, for nestlings there are no conflict between handling time and time used for other activities.

Methods to analyze diet of raptors

A disadvantage with the use of video monitoring is the difficulty of identifying small prey items. It was easier to identify small mammals, where there are fewer alternatives in Norway, than small passerines. Only 30 % of the passerine prey were identified to species level. The reason could be camera angle and the quality of the recordings, as well as the fact that many birds were plucked prior to delivery and thus lacked characteristics that is needed for indentification (Redpath et al. 2001, Reif & Tornberg 2006, Zárybnická et al. 2011). For me, the angle and camera position was the largest challenge. Often the prey was visible only for a short moment and often hidden behind the nestlings, so that identifying a prey as a passerine was based on the tarsi as they were swallowed. In future studies more than one camera should be used to get a view from different angles of the nest and to maximize the probability of observing the prey. In my study, many of the passerines were identified by size and not to taxonomic levels, which can cause subjective results and is a source of bias (Tornberg & Reif 2007).

The use of indirect methods, i.e. analyzing regurgitated pellets and prey remains, found in or near the nest, to estimate diet of raptors is biased with respect to overall number of prey and the proportion of species (Lewis et al. 2004, Tornberg & Reif 2007). Both methods underestimate the number of prey (Lewis et al. 2004, Tornberg & Reif 2007). Analyzing pellets often overestimate the number of mammals and underestimate the number of avian prey, while the use of prey remains overestimate the number of large prey species and avian prey (Redpath et al. 2001, Lewis et al. 2004). More frequent visits to collect remains would reduce the bias, but some prey will still be underestimated, because remains are removed from the nest by the adult raptor (Tornberg & Reif 2007), as also observed in my study.

The direct methods, i.e. camera monitoring or direct observation, would give a more accurate estimate of the number of prey delivered and of diet composition, although at a higher taxonomic level, as the indirect methods gives a higher diversity of species (Redpath et al. 2001, Lewis et al. 2004, Tornberg & Reif 2007, García-Salgado 2015). The direct methods allow the opportunity to study other aspects of nest activity, including handling time, nestling activity and parent-offspring interactions, as well as the diet (Lewis et al. 2004, Steen 2010, Steen et al. 2010, 2011, Sonerud et al. 2013, 2014a,b). When analyzing many nests video monitoring can be less suitable than indirect methods, as it is expensive and more time-consuming, and in addition the video equipment can suffer from technical failures (Reif & Tornberg 2006, Tornberg & Reif 2007, García-Salgado 2015). Many studies suggest combining direct and indirect methods in order to give a more accurate composition of diet. However, the use of both direct and indirect methods cause more disturbance and visits during incubation or the early nestling period, which may cause desertion and should be done with high caution (Hardey et al. 2006).

Conclusion

The video monitoring and direct field observations in this study provided information about the breeding ecology, like diet, prey deliveries and handling time, in the marsh harrier at the northern border of its existence. The diet of marsh harriers in Norway consisted of vertebrate animals belonging to several classes, where birds and mammals were the main prey. Passerines were important by number, but not by mass. Water voles were the most important species by both number and biomass. My study year was a peak water vole year, indicating that the diet of marsh harriers is highly influenced by the local prey availability. I found some support of different prey selection between the female and the male. The male captured more small passerines, supporting one hypothesis for RSD in raptors, namely that males are smaller than females in order to capture small agile prey (Newton 1979). The prey handling time increased with prey mass, and the increase was faster for mammalian prey than for avian prey, indicating that small mammals and large birds are more beneficial when feeding nestlings in order to release time for the parents to hunt and self-feed. In order to investigate further the different parental roles of marsh harriers it would have been interesting to radio-track the adults during hunting to obtain more information about prey selection, in relation to habitat use and distance from the nest.

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Appendix

Appendix 1: Mean gross prey body mass is the estimated weight of the prey species at the moment at capture, as gathered from literature (Cramp 1985, 1988, 1992, Cramp & Perrins 1994, Selås 2001).

Prey category	Mean gross body mass (g)
Mallard (*Anas platyrhynchos)*	1098
Duckling (Anatidae indet.)	150
Pheasant (*Phasianus colchicus*)	1133
Moorhen (*Gallinula chloropus*)	350
Rail (Rallidae indet.)	300
Common swift (*Apus apus*)	40
Pigeon (Columbidae indet.)	475
Eurasian skylark (*Alauda arvensis*)	36
European robin (*Erithacus rubecula*)	18
Whinchat (*Saxicola rubetra*)	16
Common blackbird (*Turdus merula*)	95
Fieldfare (*Turdus pilaris*)	105
Redwing (*Turdus iliacus*)	70
Song thrush (*Turdus philomelos*)	74
Thrush indet. (*T. philomelos* or *T. iliacus*)	72
Eurasian blackcap (*Sylvia atricapilla*)	17
Garden warbler (*Sylvia borin*)	19
Warbler (*Sylvia* sp.)	14
Warbler (*Phylloscopus* sp.)	9
Warbler (Sylviidae indet)*	14
Great tit (*Parus major*)	18
Tit (*Poecile montanus or P. palustris*)	12
Eurasian jay (*Garrulus glandarius*)	158
Hooded crow (*Corvus cornix*)	509
Tree sparrow (*Passer montanus*)	23
Common chaffinch (*Fringilla coelebs*)	23
European greenfinch (*Chloris chloris*)	27
Reed bunting (*Emberiza schoeniclus*)	19
Yellowhammer (*Emberiza citrinella*)	20

* Using the old classification of Sylviidae, including *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*.

Appendix 2: Number of prey items recorded delivered at two marsh harrier nests in Norway by use of video, given as percentage by number and percentage by the estimated net prey body mass for each prey category. The net prey body mass is the estimated body mass at delivery, corrected for decapitation and partial consumption prior to delivery.

Prey	Rokkevannet			Hellesjøvannet			Total		
	N	g	%	N	g	%	N	g	%
Mountain hare (*Lepus timidus*)	19	3460	14.5	0	0	0.0	19	3460	7.2
Mice (*Apodemus* sp.)	54	1182	5.0	30	634	2.6	84	1816	3.8
Brown rat (*Rattus norvegicus)*	0	0	0.0	1	121	0.5	1	121	0.3
Bank vole (*Myodes glareolus)*	0	0	0.0	1	20	0.1	1	20	0.0
Field vole (*Microtus agrestis)*	39	1169	4.9	15	440	1.8	54	1609	3.4
Water vole (*Arvicola amphibius*)	65	6483	27.2	167	15094	62.6	232	21577	45.0
Unidentified rodents	8	247	1.0	1	23	0.1	9	270	0.6
Mammals total	185	12541	52.7	215	16332	67.8	400	28873	60.3
Mallard (*Anas platyrhynchos)*	2	824	3.5	1	366	1.5	3	1190	2.5
Duckling (Anatidae indet.)	10	1500	6.3	2	300	1.2	12	1800	3.8
Pheasant (*Phasianus colchicus*)	2	567	2.4	0	0	0.0	2	567	1.2
Moorhen (*Gallinula chloropus*)	0	0	0.0	1	100	0.4	1	100	0.2
Rail (Rallidae indet.)	0	0	0.0	1	100	0.4	1	100	0.2
Common swift (*Apus apus*)	1	40	0.2	0	0	0.0	1	40	0.1
Pigeon (Columbidae indet.)	4	950	4.0	0	0	0.0	4	950	2.0
Eurasian skylark (*Alauda arvensis*)	1	36	0.2	2	72	0.3	3	108	0.2
European robin (*Erithacus rubecula*)	2	36	0.2	0	0	0.0	2	36	0.1
Whinchat (*Saxicola rubetra*)	1	16	0.1	1	16	0.1	2	32	0.1
Common blackbird (*Turdus merula*)	3	273	1.1	7	665	2.8	10	938	2.0
Fieldfare (*Turdus pilaris*)	2	210	0.9	6	630	2.6	8	840	1.8
Redwing (*Turdus iliacus*)	1	70	0.3	0	0	0.0	1	70	0.1
Song thrush (*Turdus philomelos*)	0	0	0.0	8	560	2.3	8	560	1.2
Thrush (*T. philomelos* or *T. iliacus*)	11	792	3.2	28	2016	8.0	39	2808	5.6
Eurasian blackcap (*Sylvia atricapilla*)	3	51	0.2	1	17	0.1	4	68	0.1
Garden warbler (*Sylvia borin*)	0	0	0.0	3	57	0.2	3	57	0.1
Warbler (*Sylvia* sp.)	2	28	0.1	4	56	0.2	6	84	0.2
Warbler (*Phylloscopus* sp.)	5	45	0.2	28	252	1.0	33	297	0.6
Warbler (Sylviidae indet)*	6	84	0.4	18	252	1.0	24	336	0.7
Great tit (*Parus major*)	3	54	0.2	1	18	0.1	4	72	0.2
Tit (*Poecile montanus or P. palustris*)	0	0	0.0	1	12	0.0	1	12	0.0
Eurasian jay (*Garrulus glandarius*)	0	0	0.0	1	79	0.3	1	79	0.2
Hooded crow (*Corvus cornix*)	2	424	1.8	1	127	0.5	3	551	1.1
Tree sparrow (*Passer montanus*)	5	115	0.5	1	23	0.1	6	138	0.3
Common chaffinch (*Fringilla coelebs*)	2	46	0.2	2	46	0.2	4	92	0.2
European greenfinch (*Chloris chloris*)	0	0	0.0	3	81	0.3	3	81	0.2
Reed bunting (*Emberiza schoeniclus*)	5	95	0.4	3	57	0.2	8	152	0.3
Yellowhammer (*Emberiza citrinella*)	18	540	2.3	14	420	1.7	32	960	2.0
Unidentified passerines	233	4339	18.1	48	870	3.6	281	5187	10.8
Passerines total	305	7232	30.3	181	6326	25.8	486	13158	28.0
Birds total	325	11113	46.6	185	7192	29.4	510	18305	38.0

Frog (*Rana* sp.)	7	175	0.7	1	25	0.1	8	200	0.4
Amphibians total	7	175	0.7	1	25	0.1	8	200	0.4
Viviparous lizard (*Lacerta vivipara*)	1	5	0.0	0	0	0.0	1	5	0.0
Reptiles total	1	5	0.0	0	0	0.0	1	5	0.0
Common bream (*Abramis brama*)	0	0	0.0	2	652	2.7	2	652	1.4
Fish total	0	0	0.0	2	652	2.7	2	652	1.4
Total	539	23812	100.0	409	24103	100.0	948	47915	100.0

* Using the old classification of Sylviidae, including *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*.

Appendix 3: Number of prey items recorded delivered at two marsh harrier nests in Norway by use of video monitoring, given as percentage by number for each prey category captured by the females and males separately.

Prey	Female		Male		Total	
	N	%	N	%	N	%
Mountain hare (*Lepus timidus*)	10	3.1	9	1.5	19	2.1
Mice (*Apodemus* sp.)	31	9.7	50	8.4	81	8.8
Brown rat (*Rattus norvegicus)*	0	0.0	1	0.2	1	0.1
Bank vole (*Myodes glareolus)*	0	0.0	1	0.2	1	0.1
Field vole (*Microtus agrestis)*	14	4.4	35	5.9	49	5.3
Water vole (*Arvicola amphibius*)	101	31.5	126	21.1	227	24.8
Unidentified rodents	4	1.2	4	0.7	8	0.9
Mammals total	160	49.8	226	37.9	386	42.1
Mallard (*Anas platyrhynchos)*	3	0.9	0	0.0	3	0.3
Duckling (Anatidae indet.)	10	3.1	2	0.3	12	1.3
Pheasant (*Phasianus colchicus*)	1	0.3	1	0.2	2	0.2
Moorhen (*Gallinula chloropus*)	1	0.3	0	0.0	1	0.1
Rail (Rallidae indet.)	0	0.0	1	0.2	1	0.1
Common swift (*Apus apus*)	1	0.3	0	0.0	1	0.1
Pigeon (Columbidae indet.)	1	0.3	3	0.5	4	0.4
Eurasian skylark (*Alauda arvensis*)	0	0.0	3	0.5	3	0.3
European robin (*Erithacus rubecula*)	1	0.3	1	0.2	2	0.2
Whinchat (*Saxicola rubetra*)	1	0.3	1	0.2	2	0.2
Common blackbird (*Turdus merula*)	4	1.2	5	0.8	9	1.0
Fieldfare (*Turdus pilaris*)	4	1.2	4	0.7	8	0.9
Redwing (*Turdus iliacus*)	1	0.3	0	0.0	1	0.1
Song thrush (*Turdus philomelos*)	0	0.0	8	1.3	8	0.9
Thrush (*T. philomelos* or *T. iliacus*)	13	4.0	25	4.2	38	4.1
Eurasian blackcap (*Sylvia atricapilla*)	2	0.6	2	0.3	4	0.4
Garden warbler (*Sylvia borin*)	0	0.0	3	0.5	3	0.3
Warbler (*Sylvia* sp)	1	0.3	5	0.8	6	0.7
Warbler (*Phylloscopus* sp)	6	1.9	26	4.4	32	3.5

Warbler (Sylviidae indet)*	7	2.2	17	2.9	24	2.6
Great tit (*Parus major*)	0	0.0	4	0.7	4	0.4
Tit (*Poecile montanus or P. palustris*)	0	0.0	1	0.2	1	0.1
Eurasian jay (*Garrulus glandarius*)	0	0.0	1	0.2	1	0.1
Hooded crow (*Corvus cornix*)	0	0.0	3	0.5	3	0.3
Tree sparrow (*Passer montanus*)	1	0.3	4	0.7	5	0.5
Common chaffinch (*Fringilla coelebs*)	0	0.0	4	0.7	4	0.4
European greenfinch (*Chloris chloris*)	2	0.6	1	0.2	3	0.3
Reed bunting (*Emberiza schoeniclus*)	2	0.6	6	1.0	8	0.9
Yellowhammer (*Emberiza citrinella*)	8	2.5	21	3.5	29	3.2
Unidentified passerines	75	23.4	196	32.9	271	29.6
Passerines total	129	40.2	345	57.9	474	51.7
Birds total	146	45.5	352	59.1	498	54.3
Frog (*Rana* sp)	1	0.3	6	1.0	7	0.8
Amphibians total	1	0.3	6	1.0	7	0.8
Common bream (*Abramis brama*)	2	0.6	0	0.0	2	0.2
Fish total	2	0.6	0	0.0	2	0.2
Unidentified prey	11	3.4	12	2.0	23	2.5
Total	321	100.0	596	100.0	917	100.0

* Using the old classification of Sylviidae, including *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*.

** The viviparous lizard (*Lacerta vivipara*) was captured by one of the nestlings.

Appendix 4: Parameter estimates of the best model for table 6, figure 2, M_{4a}, for mammalian prey.

Explanatory variable	Estimate	SE	z	p
Intercept	-2.403	0.331	-7.265	<0.001
I(cos(2 * π * Hour/24))	-2.916	0.367	-7.909	<0.001
I(sin(2 * π * Hour/24))	-0.778	0.156	-4.997	<0.001
I(cos(2 * 2 * π * Hour/24))	-1.429	0.245	-5.836	<0.001
I(sin(2 * 2 * π * Hour/24))	-1.059	0.194	-5.449	<0.001
I(cos(3 * 2 * π * Hour/24))	-0.538	0.145	-3.705	<0.001
I(sin(3 * 2 * π * Hour/24))	-0.505	0.150	-3.354	<0.001

Appendix 5: Parameter estimates of the best model for table 6, figure 2, M_{4b}, for avian prey.

Explanatory variable	Estimate	SE	z	p
Intercept	-2.341	0.240	-9.760	<0.001
I(cos(2 * π * Hour/24))	-2.937	0.382	-7.687	<0.001
I(sin(2 * π * Hour/24))	-1.042	0.163	-6.408	<0.001
I(cos(2 * 2 * π * Hour/24))	-1.473	0.252	-5.849	<0.001
I(sin(2 * 2 * π * Hour/24))	-0.811	0.199	-4.083	<0.001
I(cos(3 * 2 * π * Hour/24))	-0.327	0.146	-2.244	0.045
I(sin(3 * 2 * π * Hour/24))	-0.232	0.149	-1.559	0.119

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