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Prey Delivery and Handling at the Nest in Ospreys (*Pandion haliaetus*): Diel Patterns and Potential Family Conflicts

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Abstract

The prey items delivered at four osprey (*Pandion haliaetus*) nests in Østfold county, Norway, and the handling of these, were recorded on video during the nestling season in June-August of 2015. A total of 510 prey items were recorded, of which 491 were identified to order, family or species level, while the remaining 19 prey items were only identified as fish. Carps (*Cyprinidae* sp.) were delivered most frequently (38.8%), while flounders (*Pleuronectidae* sp.), perches (*Percidae* sp.), mackerels (*Scombridae* sp.) and pikes (*Esocidae* sp.) were the other most common prey types by number (16.3%, 11.4%, 6.9% and 6.5%, respectively). At species level freshwater bream (*Abramis brama*), European flounder (*Platichthys flesus*), European perch (*Perca fluviatilis*), Atlantic mackerel (*Scomber scombrus*) and Northern pike (*Esox lucius*) were the most frequently delivered prey, and contributed with 48.2%, 12.0%, 8.5%, 5.4% and 6.0% to the total estimated prey body mass at capture, respectively. There was, however, a significant difference in delivered prey species between the nests. The probability of a prey delivery within an hour block was high during daylight, and especially high in the hour blocks between 07:00-09:00 and 17:00-19:00. The diel pattern of deliveries for the different types of prey items seemed to be partly determined by the ospreys' hunting premises and partly determined by the assumed activity patterns of the prey type. In addition to the time of the day, the delivery of mackerels at the nest was strongly affected by the tidal cycle and wind speed. The male delivered 92.3% of all prey items, while the female dismembered prey items in all the cases where the nestlings received feeding assistance. The probability of assisted feeding decreased with increasing nestling age and increased with increasing prey mass. The nestlings were equally likely to feed unassisted as assisted on prey of average size at an age of 51 days. Mackerels were more likely to be delivered at the nest partially consumed, i.e. with more than just the head lacking, while perches were less likely so, compared to the other most commonly delivered prey types. Perches were also less likely to be delivered decapitated at the nest compared to the other prey types, and heavier prey were more likely to be decapitated prior to delivery than prey with a lower estimated body mass. The amount of prey received per nestling per monitored hour block during the nestling season decreased slightly throughout the monitoring period.

Sammendrag

Byttedyrleveringene ved fire fiskeørnreir (*Pandion haliaetus*) i Østfold fylke, Norge, og håndteringen av disse, ble videoovervåket gjennom hekkesesongen i 2015. Til sammen ble 510 byttedyrleveranse filmet, hvorav 491 ble bestemt til orden, familie eller art, mens de resterende 19 byttedyrene kun ble identifisert som fisk. Karpefisker (*Cyprinidae* sp.) ble levert oftest (38.8%), mens flyndrefisker, (*Pleuronectidae* sp.), abborfisker (*Percidae* sp.), makreller (*Scombridae* sp.) og gjeddefisker (*Esocidae* sp.) var de andre vanligste byttedyrtypene ut i fra antall (henholdsvis 16.3%, 11.4%, 6.9% of 6.5%). På artsnivå var brasme (*Abramis brama*), skrubbeflyndre (*Platichthys flesus*), abbor (*Perca fluviatilis*), makrell (*Scomber scombrus*) og gjedde (*Esox lucius*) de oftest leverte byttedyrene, og bidro med henholdsvis 48.2%, 12.0%, 8.5%, 5.4 og 6.0% til den totale estimerte fangede byttedyrmassen. Det var imidlertid en signifikant forskjell i leverte byttedyrarter mellom reirene. Sannsynligheten for at et byttedyr ble levert innen en timesblokk var høy så lenge det var dagslys, og spesielt høy i timesblokkene mellom 07:00-09:00 og 17:00-19:00. Aktivitetsmønsteret for leveringer av de ulike byttedyrtypene syntes å være dels styrt av fiskeørnas jaktforutsetninger og dels styrt av byttedyrtypenes antatte aktivitetsmønster. I tillegg til tid på døgnet hadde leveringene av makrell på reiret en sterk sammenheng med tidevannssyklus og vindstyrke. Hannen leverte 92.3% av alle byttedyrene, mens hunnen parterte byttedyrene i alle de tilfellene hvor ungene mottok assistanse. Sannsynligheten for assistert spising minsket med økende alder på ungene og økte med økende byttedyrmasse. Det var like sannsynlig at ungene spiste uassistert som assistert på byttedyr av gjennomsnittlig størrelse når de var 51 dager gamle. Makreller hadde høyere sannsynlighet for å bli levert delvis påspist (mer enn bare hodet), mens abborer hadde en lavere sannsynlighet, sammenlignet med de andre vanligste byttedyrtypene. Abborer hadde også en lavere sannsynlighet for å bli levert dekapitert på reiret sammenlignet med de andre byttedyrtypene, og tyngre byttedyr hadde større sannsynlighet for å være påspist enn byttedyr med en lavere estimert kroppsvekt. Mengden mat mottatt per unge per overvåkede timesblokk minket noe gjennom hekkesesongen som en respons av sesong.

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1 Introduction

The diet of most raptors, i.e. hawks, falcons and owls is regarded as fairly well known. However, this knowledge is almost solely based on analysis of pellets and prey remains collected at and around the nests, and it is not known how well these analyses reflect the actual diet. Traditional analyses of diets in birds of prey based on collections of prey remains (birds and mammals) do however indicate that the amount of larger prey species in the diet are overestimated because large prey leave more remains compared with smaller prey (Slagsvold et al. 2010). Häkkinen (1978) claims this also applies to fish eating species, such as the osprey (*Pandion haliaetus*), based on his analyses of prey remains and carcasses. Video recordings have previously been used to study the diets of 14 different species of owls, hawks and falcons, including two nests of the golden eagle (*Aquila chrysaetos*). These recordings have proven to provide an excellent method when it comes to identifying prey delivered from the parents to the nestlings all the way down to the species level (Steen et al. 2010, 2012, Sonerud et al. 2014a, b, Dihle 2015, Moen 2015, Nygård 2015).

All species are fundamentally affected by their circadian activity rhythm, as an adaptation to their environment (Erkert & Kappeler 2004). Most species are adapted to be either diurnal or nocturnal, as a result of ecological and physiological trade-offs (Erkert & Kappeler 2004). Daylength, temperatures, food availability, and inter – and intraspecific interactions are among the factors that may affect the diel pattern of a species or an individual (Pita et al. 2011). Thus, decisions associated with foraging, are closely linked to a species' activity rhythm.

In addition to a species' circadian activity rhythm affecting prey choice, optimal foraging theory predicts how predators should make decisions when hunting and allocating prey (Stephens & Krebs 1986). According to the theory, the providing parent should select and handle each prey to maximize the net energy gain per time unit, when taking the costs of prey handling into account, i.e. capture time, preparation time and ingestion time (Stephens & Krebs 1986, and references therein). The providing parent (usually the male) first has to decide which prey to deliver at the nest, and which prey to feed upon at the capture site (Sonerud 1992, Ydenberg 1994). Raptors are single-prey loaders, and should therefore be expected to capture and deliver relatively large prey at the nest in order to reduce the relative costs of transportation from the hunting site (Sonerud 1992). The providing parent also has to make decisions about whether or not to prepare the prey item prior to transport. Such preparations may include removing parts with low energetic value to increase the net nutrient concentration (Kaspari 1990), or to generally reduce the costs of transport by reducing the weight of the prey item (Rands et al. 2000). When the prey item has been delivered at the nest, the sedentary parent (usually the female) has to decide whether or not to assist the nestlings in their feeding. When assisting, the female has the power to allocate food between her nestlings, and at the same time decide how much to eat herself (Sonerud et al. 2013). Thus, the female's role at the nest may be the basis for a family conflict, where she has the ability to exploit more than her fair share, at the expense of her mate (Eldegard & Sonerud 2009, 2010). On the other hand, leaving the female to assist may also maximize the nestlings' ingestion efficiency and allow the male to maximize his foraging time by allowing him to return quickly to the hunting site (Slagsvold & Sonerud 2007).

The osprey is a medium sized diurnal raptor (1400-2000 g, wing span 145-170 cm, the female 5-10 % larger than the male) specialized on catching fish, and has been observed to capture a wide diversity of fish species by using different diving techniques. The osprey is a visual hunter, and dives in shallow water or in the upper water layers (approximately down to 1 m) and captures prey items in its talons after spotting it from the air (Cramp & Simmons 1979). Ospreys breed on all continents, except South-America and Antarctica. In the northern parts of the Palearctic they usually build their nests in the top of a Scots pine (*Pinus sylvestris*) (Cramp & Simmons 1979). Artificial nest platforms have however been successful in the recolonization project in Scotland (Dennis 2008). In Norway the osprey is a migratory bird, staying from April to September, and mainly wintering in western Africa (Cramp & Simmons 1979). They are believed to form seasonal monogamous bonds, and the female lays 1-4 eggs asynchronously (Cramp 1979 & Simmons). Nestling care is biparental, but strongly differentiated. During the breeding season the male is assumed to be the main food provider, while the female broods, feeds and defends the nest area (Cramp & Simmons

1979). The male may range 10-20 km from the nest to forage, and can catch prey as heavy as >1 kg, although traditional prey remain analyses report an average prey mass of 200-300 g (Nordbakke 1974, 1980, Cramp & Simmons 1979).

For ospreys nesting in Norway the diet throughout the nestling season is poorly known, except for a population nesting in small lakes in the southeastern parts of Østfold county, where a larger study was conducted in 1972-1973. The study was based on the collection of 690 prey remains from approximately ten different nests, and found that 9 out of 24 freshwater fish species in the area were present among the recorded prey species (Nordbakke 1974, 1980). The most common prey species recorded were ide (*Leuciscus idus*), pike (*Esox lucius*) and perch (*Perca fluviatilis*), which accounted for 73% of all the prey items recorded (Nordbakke 1974, 1980).

Prior studies on the Eurasian kestrel (*Falco tinnunculus*) using video recordings have shown that the size of the prey affects whether the female dismembers and feeds the nestlings, or if the nestlings feed without help from the mother (Sonerud et al. 2014b). Weather conditions also seem to affect what type of prey that is delivered at the nest in this species (Steen et al. 2011). Studies on the golden eagle and the Ural owl (*Strix uralensis*) have shown that prey type, prey body mass and nestling age affected whether the female dismembers and feeds the nestlings rather than the nestlings ingesting prey unassisted (Nygård 2015, Moen 2015).

With the use of video recordings at osprey nests several aspects of behavior can be investigated more thoroughly and accurately than before. The objectives of this study was as follows: 1) How is the diet composition at these nests during the nestling season, and to what extent does it differ between the nests located by the coast and inland? 2) Which factors (e.g. ambient temperature, wind, tide and time of day) affect the type of prey (e.g. species) delivered at the nest? 3) Which factors affect whether the female dismembers the prey or the nestlings ingest the prey independently? 4) Which factors affect whether a prey is decapitated or even more eaten at prior to being delivered at the nest? 5) Which factors affect the feeding effort, i.e. the amount of prey delivered at the nest throughout the nestling period?

2 Methods

2.1 Study area

The study was conducted at four different osprey nests in Østfold county, Norway, during June-August in 2015. The sites, termed Leiret, Isnes, Huseby and Elinborg (figure 1), were selected with the help of local collaborators from the ornithology association in Østfold county, who have monitored the nests for several seasons. Each of the four nests was placed in the top of a scots pine in areas with mixed coniferous and deciduous forests.

The river Glomma, Norway's longest, runs through the study area. This river splits into an eastern and a western path just north of the nest at Isnes (figure 1). The eastern path forms the main part of the river, which runs south through the town Sarpsborg (Thorsnæs 2015). The western path runs through the lakes Mingevannet and Vestvannet, and a third path of the river (also called Ågårdselva) exits the lake Vestvannet, and runs through the lakes Visterflo and Skinnerflo. The river Seutelva exits Skinnerflo and enters into the river Vesterelva, which exits into the Oslo fiord. Visterflo exits into Glomma by Rolvsøy, where the eastern and western paths come together, and flow south into the outer parts of the Oslo fiord by the town Fredrikstad (figure 1). The lower parts of Glomma contain brackish water, which explains why the Atlantic cod (*Gadus morhua*) occurs there (table 1). The lakes Tunevannet and Vansjø are other freshwater lakes of some size in the area. Saltwater fishing localities are also accessible for the ospreys from all the nest sites, as the shortest distance from the nests to saltwater range from 1.5 km (Elinborg) to 14 km (Isnes). The different fish species registered in the freshwater lakes and rivers mentioned above are listed in table 1.

Table 1: Fish species recorded in freshwater lakes and rivers (see text) in the area around the osprey nest sites (Turkart Østfold 2016).

	Rivers			Freshwater lakes					
Species	Glomma	Ågårdselva	Seutelva	Visterflo	Skinnerflo	Vestvannet	Tunevannet	Mingevannet	Vansjø
Roach (*Rutilus rutilus*)	x	x	x	x	x	x	x	x	x
Pike (*Esox Lucius*)	x	x	x	x	x	x	x	x	x
Perch (*Perca fluviatilis*)	x	x	x	x	x	x	x	x	x
Bleak (*Alburnus alburnus*)	x	x	x	x	x	x	x	x	x
European eel (*Anguilla anguilla*)	x	x	x	x	x	x	x	x	x
Rudd (*Scardinius erythrophthalmus*)	x	x	x	x	x	x	x	x	x
Freshwater bream (*Abramis brama*)	x	x	x	x	x	x		x	x
White bream (*Blicca bjoerkna*)	x	x	x	x	x	x		x	x
Ruffe (*Gymnocephalus cernua*)	x	x	x	x	x	x	x	x	
Pike-perch (*Sander lucioperca*)	x		x	x	x	x	x	x	x
Trout (*Salmo trutta*)	x	x	x	x	x			x	
Ide (*Leuciscus idus*)	x		x	x	x	x		x	
Common dace (*Leuciscus leuciscus*	x				x				
Chub (*Scualius cephalus*)	x	x	x	x	x	x		x	
Burbot (*Lota lota*)	x	x	x	x	x			x	x
Alpine bullhead (*Cottus poecilopus*)	x								
Grayling (*Thymallus thymallus*)	x								
Vendace (*Coregonus albula*)	x					x		x	
European smelt (*Osmerus eperlanus*)	x					x		x	x
European whitefish (*Coregonus lavaretus*)	x								
Atlantic cod (*Gadus morhua*)	x	x	x	x	x	x		x	
Tench (*Tinca tinca*)									x

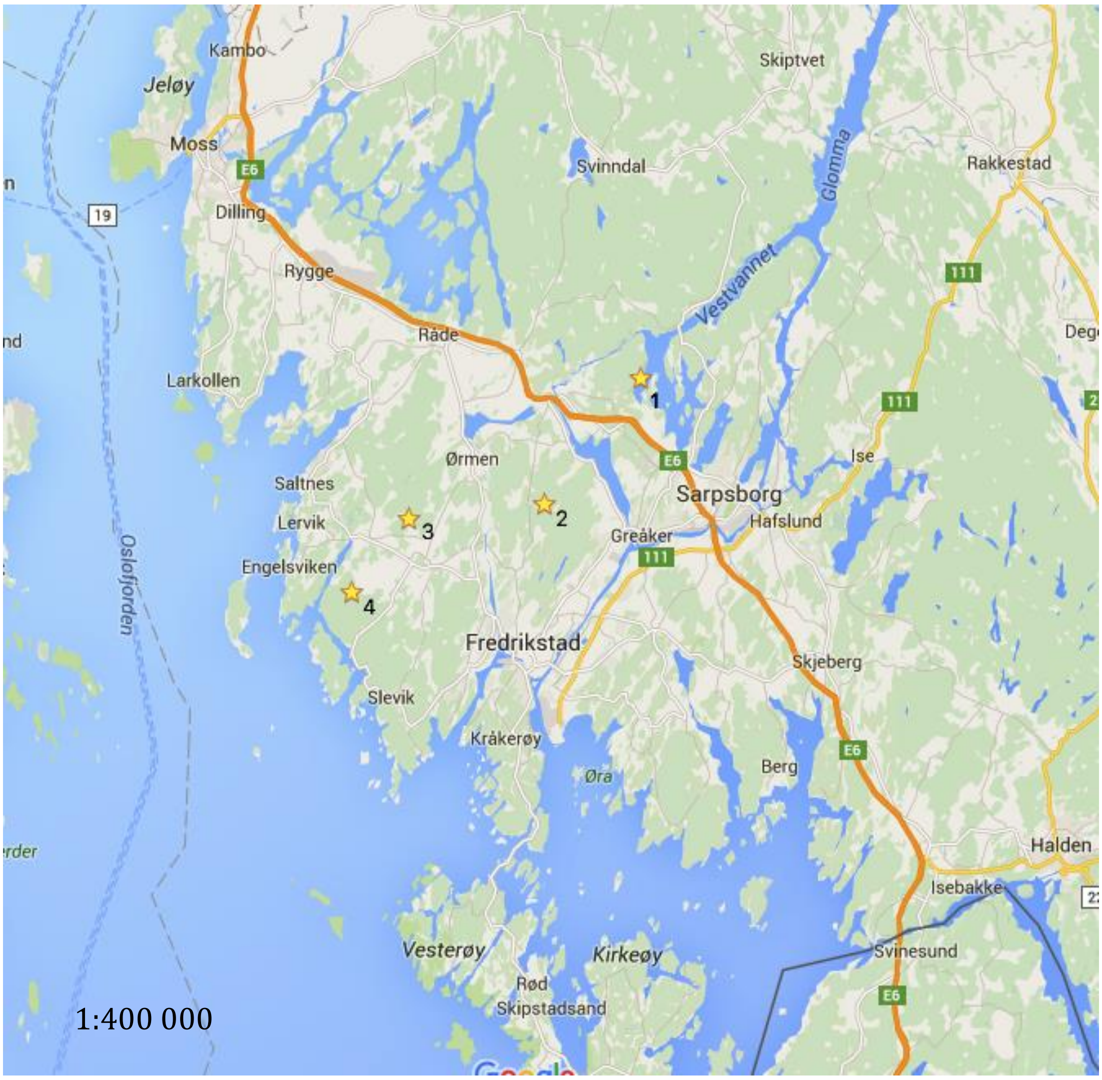


Figure 1: The locations of the osprey nest sites in Østfold county. 1: Isnes, 2: Leiret, 3: Huseby, 4: Elinborg (Google Maps 2016).

Elinborg was the only nest site closer to the coast than to a freshwater lake or river (6.5 km). Isnes was located right by the shoreline of the lake Vestvannet, while Leiret and Huseby were approximately 2.5 km and 3.5 away from the closest freshwater fishing locality, respectively.

The nests were located close to human settlements, approximately 0.5 km at Elinborg, 0.6 km at Isnes, 0.2 km at Leiret and 0.8 km at Huseby, but very little human activity was observed close by the nests during the field work. Sound of traffic and other human activities could however be heard at all the sites regularly.

2.2 Video recording

To avoid disturbing the ospreys when they started their nesting, the recording equipment used to monitor prey deliveries was initially installed in the end of March and beginning of April at Huseby, Leiret and Isnes, before the ospreys arrived from their winter migration. The recordings were started as soon as the nestlings had hatched in the beginning of June at Huseby and Leiret, while technical difficulties at Isnes delayed the recordings until 26 June. The nestlings at the latter nest hatched some time later than the other nests, so they were still only eight days old when the recordings started. The equipment used at Huseby was moved to Elinborg on 26 June, because both nestlings at the former nest had fallen down through a hole in the nest and succumbed on 18 June. Nestling age at Elinborg and Isnes was estimated by comparing recordings from these nests with recordings of the nestlings at Huseby and Leiret, where the exact nestling age was known.

The camera setup used at all the sites consisted of a wideangle miniature camera installed on a pole that was fastened to the edge of the nest. The camera was connected to a digital video recorder (DVR) of the type Secumate H.264 Mini Portable DVR through an approximately 100 m long video cable. This allowed operating the DVR device during the field season without having to visit the nest and disturbing the birds severely. The cable was also connected to a 12V lead battery that provided the power for both the camera and the DVR recorder. The motion detection settings of the DVR recorder was set in such a way that movements at the nest triggered 10 s long recordings that were saved as .avi-files on an SD-card. In addition, recordings 5 s prior to the movements that triggered the recording were stored on the SD-card. To ensure that all prey deliveries got recorded, the SD-cards had to be changed every day during the nestling period and every 2-3 days after the young fledged the nest. The battery had to be changed every 8-9 days throughout the entire period. This setup was a modified version of that described by Steen (2009) for studies on the Eurasian kestrel (*Falco tinnunculus*), and has been used to successfully monitor prey deliveries in several raptor species (e.g. Sonerud et al. 2014a).

At Leiret, continuous recordings during the study period were prevented by two incidents of the nestlings eliminating on the camera lens and one incident of poor connection between the camera and DVR recorder. Also, some breaks in the recordings occurred at all the sites because logistic constraints sometimes prevented changing the SD-cards at the time needed.

2.3 Video analysis

Prey species identification

All recordings were analyzed on a computer screen, first to find all prey deliveries, and then to record associated date and time. The time was recorded as when the delivering parent landed with the prey on the nest. Each prey was then identified to order, family and species when possible. A fish handbook (Nielsen 2011) was used as a reference in this work. In the three cases of more than one fish delivered at the same time, the prey were still recorded as one delivery to avoid statistical problems. In all these cases, both fish were of the same species. Some prey could not be identified to any taxonomic level due to the nature of the recordings. This was especially the case at Leiret in the periods 26 June – 9 July and 11 – 25 July, due to feces from the young covering the camera lens.

Estimation of prey length and prey mass

When installing the recording equipment, a metal grid was put on top of each nest temporarily when the camera was mounted, and then recorded and removed (figure 2). Each square of the grid measured 7.5 cm x 7.5 cm, so the diagonal length of each square was 10.5 cm. A still picture from each of these recordings was displayed on a computer screen, then drawn on to a transparent plastic sheet, and later put on top of the computer screen for every prey delivery as a size reference. The length of each delivered prey item was estimated by determining the number of squares it covered to the closest quarter from a still picture, in which they laid straight across or diagonally compared to the squares in the grid. When a fish did not cover a precise quarter square, its length was truncated down to the closest quarter square, giving a conservative measure of the prey length. Since the nest bowl changed from very hollow to almost flat during the breeding season, these measurements could not be done with complete accuracy. The length of some fish could not be determined because they could not be seen properly due to lack of visualization or the way they were positioned in the nest in relation to the squares of the reference grid.

Figure 2: Metal grid used to estimate the length of the prey items delivered at the osprey nests.

Some of the fish were decapitated or half eaten prior to delivery at the nest. By measuring the snout-tail length from illustrations in Nielsen (2011) and drawing lines for each quarter of the fish illustrated, I estimated each prey item delivered to the nearest quarter part of the whole fish by comparing the shapes and proportions. The length of the delivered item was divided by its proportion of a whole fish to find the length of the fish at capture. When a delivered fish was not a complete quarter part, it was truncated up to the nearest quarter. This contributed to a conservative measure of the length of the fish that were actually captured by the delivering parent.

The mass of a delivered fish was found by using the length-weight tables for each species. These tables use the formula

$$W = a \times L^b$$

to estimate mass (Froese & Pauly 2016a, and references therein) . In the equation above W is fish mass (g), L is fish length (cm), while a and b are species specific coefficients. To find the mass of a delivered prey that was decapitated or otherwise eaten at prior to delivery, I multiplied the mass of the captured fish with the proportion of fish delivered. Because the head of a fish is generally very heavy compared to it's tail, the estimated mass of the prey that were decapitated or otherwise eaten at prior to delivery are somewhat overestimated.

Weather and tide

Hourly data on ambient temperature (°C) and wind speed (m/s) were found at the data base eKlima (2016) from the Norwegian Meteorological Institute for the entire period. The weather station at Rygge (station number 17150) was used for Leiret and Isnes (approximately 21 km and 23 km away from the associated nests, respectively), while the weather station at Strømtangen fyr (station number 17000) was used for Huseby and Elinborg (approximately 13 km and 10 km away from the associated nests, respectively). Different stations were used to ensure as accurate data as possible for each study site.

Hourly data on observed tide was found at the Norwegian Mapping Authority (2016) for Viker station, outside of Hvaler in the Oslo fiord. The data are given in cm as a deviation from the lowest astronomical tide (LAT).

Norwegian summer time (UTC+2) is not taken into account at either eKlima or the Norwegian Mapping Authority. Therefore, an extra column was added to the data set, where the time of each prey delivery was adjusted back one hour (UTC+1) to match the weather and tidal data for analytic purposes. In addition, the prey delivered between 00:00 and 01:00 had to be adjusted one day back, and the deliveries within this hour at the last day of the month had to be adjusted one month back in additional columns in the data set.

In the middle of the study period, on 13 July, the sun rose at 05:02 and set at 21:28, and solar midday occurred at 13:15, in the study area.

2.4 Statistical analyses

The statistical analyses containing nest ID as random effect were conducted in R (2015) version 3.2.3., and the analyses without nest ID as random effect were conducted in JMP Pro 10.0 (SAS Institute 2012).

Differences in delivered prey species between the nests

A contingency analysis was used to test for differences in delivered prey species between the nests, based on deliveries of the five most common prey species among all prey delivered.

A one-way analysis of variation was used to test for differences in the average estimated prey body mass between the different nests, both for all delivered prey items and for the five most common prey species among all prey delivered.

Diel activity

The COSINOR method (Pita et al. 2011) was used to analyze the daily activity rhythm for all prey deliveries in general and for each prey family that was represented in more than 30 prey deliveries. The "lme4"(Bates et al. 2014) and "AICcmodavg" (Mazerolle 2016) packages were used to create generalized linear mixed effects models and model selections. The response variable was whether or not there was at least one prey delivery within a given hour block (yes/no). The time of day (hour blocks), tide, wind speed and temperature were the explanatory variables. Nest ID was added as a random effect to control for potential variation between each nest. The specified activity models are described in table 2.

The best model was selected by assessing Akaike information criterion values (Akaike 1978). All models within a ΔAICc interval of 2.0 from the best ranked model were considered competing (Burnham & Anderson 2002). In addition, the model within this interval that had the lowest number of fixed effects was considered to be the best fit. Only models where the explanatory variables had a p-value ≤ 0.1 were assessed further.

Table 2: The specified activity models used in the diel activity analyses of prey deliveries at the osprey nests monitored. X = the time of day (hour blocks), ε = random effect (nest ID), FF = wind speed (m/s), TA = temperature (°C), tide = lowest astronomical tide (cm).

Model no.	Variables in model
0	$f(x) = a_0 + \varepsilon$
1	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + \varepsilon$
2	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + \varepsilon$
3	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + (a_3 \cos\frac{3\ast 2\pi x}{24} + b_3 \sin\frac{3\ast 2\pi x}{24}) + \varepsilon$
4	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + TA + \varepsilon$
5	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + TA + \varepsilon$
6	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + (a_3 \cos\frac{3\ast 2\pi x}{24} + b_3 \sin\frac{3\ast 2\pi x}{24}) + TA + \varepsilon$
7	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + FF + \varepsilon$
8	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + FF + \varepsilon$
9	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + (a_3 \cos\frac{3\ast 2\pi x}{24} + b_3 \sin\frac{3\ast 2\pi x}{24}) + FF + \varepsilon$
10	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + Tide + \varepsilon$
11	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + Tide + \varepsilon$
12	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + (a_3 \cos\frac{3\ast 2\pi x}{24} + b_3 \sin\frac{3\ast 2\pi x}{24}) + Tide + \varepsilon$
13	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + Tide + FF + \varepsilon$
14	$f(x) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2\ast 2\pi x}{24} + b_2 \sin\frac{2\ast 2\pi x}{24}) + Tide + FF + \varepsilon$

15	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24}) + (a_3 \cos \frac{3*2\pi x}{24} + b_3 \sin \frac{3*2\pi x}{24}) + \text{Tide} + \text{FF} + \varepsilon$
16	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + \text{TA} + \text{FF} + \varepsilon$
17	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24}) + \text{TA} + \text{FF} + \varepsilon$
18	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24}) + (a_3 \cos \frac{3*2\pi x}{24} + b_3 \sin \frac{3*2\pi x}{24}) + \text{TA} + \text{FF} + \varepsilon$
19	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + \text{TA} + \text{Tide} + \varepsilon$
20	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24}) + \text{TA} + \text{Tide} + \varepsilon$
21	$f(x) = a_0 + (a_1 \cos \frac{2\pi x}{24} + b_1 \sin \frac{2\pi x}{24}) + (a_2 \cos \frac{2*2\pi x}{24} + b_2 \sin \frac{2*2\pi x}{24}) + (a_3 \cos \frac{3*2\pi x}{24} + b_3 \sin \frac{3*2\pi x}{24}) + \text{TA} + \text{Tide} + \varepsilon$
22	$f(x) = a_0 + \text{TA} + \varepsilon$
23	$f(x) = a_0 + \text{Tide} + \varepsilon$
24	$f(x) = a_0 + \text{FF} + \varepsilon$
25	$f(x) = a_0 + \text{TA} + \text{Tide} + \varepsilon$
26	$f(x) = a_0 + \text{TA} + \text{FF} + \varepsilon$
27	$f(x) = a_0 + \text{FF} + \text{Tide} + \varepsilon$

Prey handling

The “lme4” (Bates et al. 2014) and “AICcmodavg” (Mazerolle 2016) packages were used to create generalized linear mixed effects models of factors affecting prey handling and model selections. Two sets of analyses were run for each of the three response variables feeder (female or nestling), partial prey consumption prior to delivery at the nest (yes/no) and decapitation of prey prior to delivery at the nest (yes/no), i.e. 6 analyses in total. All analyses included nest ID as random effect to control for potential variation between each nest. The first set of analyses included fish family and nestling age as explanatory variables for each of the response variables, and the dataset analyzed included the five most common fish families represented among prey delivered at the nest (table 3a). The second set of analyses included prey mass and nestling age as explanatory variables, and the dataset analyzed included prey mass for all delivered prey at the nest (table 3b).

The best model in each set of analyses was selected by assessing AICc-values as described for the diel activity analyses above, and assessed further. In addition, the results of both sets of analyses were compared with each other.

Table 3: The linear mixed effect models used in the analyses of prey handling at the osprey nests monitored. ε = random effect (nest ID), x_1 = prey family, x_2 = nestling age, x_3 = prey mass.

Model no.	Variables in model
(a)	
1	$f(x) = a_0 + \varepsilon$
2	$f(x) = a_0 + x_1 + \varepsilon$
3	$f(x) = a_0 + x_2 + \varepsilon$
4	$f(x) = a_0 + x_1 + x_2 + \varepsilon$
(b)	
1	$f(x) = a_0 + \varepsilon$
2	$f(x) = a_0 + x_3 + \varepsilon$
3	$f(x) = a_0 + x_2 + \varepsilon$
4	$f(x) = a_0 + x_2 + x_3 + \varepsilon$

Feeding effort

The ”nlme” package (Pinheiro et al. 2016) was used to make both linear and non-linear mixed effect models of factors affecting feeding effort (table 4). The response variable was the amount of prey (g) received per nestling at the nest per monitored hour block. Both nestling age and Julian date were tested as explanatory variables in separate models to investigate whether a potential change in feeding effort was caused by a seasonal effect (i.e. a seasonal change in prey availability) or by nestling age alone. The response variable was $\log_{10}$-transformed in an attempt to achieve normal distribution. It is important to note that the prey masses reported are not adjusted for the female also feeding on prey delivered at the nest. The amount of prey received per nestling at the nest per monitored hour block is therefore somewhat overestimated.

Table 4: Linear and non-linear mixed effect models specified to find the effect of nestling age and Julian date on feeding effort of the ospreys, i.e. the amount of prey (g) received per nestling at the nest per monitored hour block. x_1 = nestling age, x_2 = Julian date, ε = random effect (nest ID).

Model no.	Variables in model
1	$\log_{10}(f(x)) = \beta_0 + \beta_1 x_1 + \varepsilon$
2	$\log_{10}(f(x)) = \beta_0 + \beta_1 x_2 + \varepsilon$
3	$\log_{10}(f(x)) = \beta_0 + \beta_1 x_1 + \beta_1 x_1^2 + \varepsilon$
4	$\log_{10}(f(x)) = \beta_0 + \beta_1 x_2 + \beta_1 x_2^2 + \varepsilon$

Seasonal distribution of prey items

Changes in the daily number of deliveries of each of the five most common prey species among all prey species delivered throughout the nestling season (i.e. Julian date) were analyzed with Poisson regression. The effect of Julian date was corrected for nest ID. The analyses were also checked for over dispersion, but none was found.

3 Results

3.1 Prey selection

In total, 510 prey deliveries were recorded during 2774 hours of video monitoring. All prey deliveries at the nest were identified as fish. Of these prey deliveries, 491 were identified to order and family level, 417 were identified to species level, while 19 could not be identified as anything but fish (3.7%). Carps (*Cyprinidae* sp.) were the prey type delivered most frequently, with 38.8% of items by number. Other frequently delivered prey types were flounders (*Pleuronectidae* sp.), perches (*Percidae* sp.), mackerels (*Scombridae* sp.) and pikes (*Esocidae* sp.) with 16.3%, 11.4%, 6.9% and 6.5%, respectively, of all deliveries by number (table 5).

At species level, freshwater bream (*Abramis brama*) was by far the most commonly delivered prey (28.4%). European flounder (*Platichthys flesus*) and European perch (*Perca fluviatilis*) were the second and third most commonly delivered prey (13.5% and 11.2%, respectively). These three species accounted for 48.2%, 12.0% and 8.5% of the estimated total captured prey body mass, respectively. The estimated average prey body mass ± SE at capture was 380 ± 14 g for all prey in general (range 7 g – 1533 g), 627 ± 24 g for freshwater bream (range 34 g – 1533 g), 291 ± 20 g for European flounder (range 36 g – 831 g) and 271 ± 27 g for European perch (range 11 g – 871 g) (table 5).

Prey were frequently delivered decapitated and even more eaten at. The estimated average prey body mass ± SE at delivery was 293 ± 11 g for all prey, 487 ± 20 g for freshwater bream, 225 ± 14 g for European flounder, and 239 ± 21 g for European perch (table 5).

Table 5: Prey delivered at the four osprey nests monitored, their relative contribution of each species (%), the estimated average body mass per prey (g) captured and delivered, in total (g), and relative to all prey items in total (%).

	Number of prey		Prey body mass at capture (g)			Prey body mass at delivery (g)		
Prey species	N	%	Per prey	Total	%	Per prey	Total	%
Freshwater bream (*Abramis brama)*	145	28.4	627	79611	48.2	487	61886	48.6
European flounder (*Platichthys flesus)*	69	13.5	291	19774	12.0	225	15290	12.0
European perch (*Perca fluviatilis*)	57	11.2	271	14095	8.5	239	12404	9.7
Atlantic mackerel (*Scomber scombrus*)	35	6.9	268	8848	5.4	202	6674	5.2
Northern pike (*Esox lucius*)	33	6.5	382	9941	6.0	283	7366	5.8
Roach (*Rutilus rutilus*)	18	3.5	171	2738	1.7	134	2148	1.7
Trout (*Salmo trutta*)	13	2.5	313	3751	2.3	268	3216	2.5
Common dace (*Leuciscus leuciscus*)	11	2.2	49	485	0.3	49	485	0.4
Ide (*Leuciscus idus*)	9	1.8	461	3689	2.2	304	2431	1.9
Garfish (*Belone belone*)	8	1.6	97	779	0.5	94	754	0.6
Atlantic cod (*Gadus morhua*)	6	1.2	222	1331	0.8	202	1213	1.0
Ballan wrasse (*Labrus bergylta*)	6	1.2	215	1076	0.7	196	982	0.8
White bream (*Blicca bjoerkna*)	3	0.6	347	1041	0.6	347	1041	0.8
Rudd (*Scardinius erythrophthalmus*)	1	0.4	448	448	0.3	336	336	0.3
Lemon sole (*Microstomus kitt*)	1	0.2	121	121	0.07	121	121	0.1

Pike-perch (*Sander lucioperca*)	1	0.2	416	416	0.3	416	416	0.3
Unidentified flounder sp.	64	12.5	-	-	-	-	-	-
Unidentified carp sp.	10	2.0	-	-	-	-	-	-
Unidentified prey	19	3.7	-	-	-	-	-	-
Total	510		380	165092.8		293	127384.4	

Differences in delivered prey species between the nests

At the nest at Elinborg, 56.8% of all delivered prey items were flounder species, of which 32.6% could be identified to European flounder. Mackerel and trout made up 15.3% and 5.3%, respectively. At Huseby, 32.2% of the delivered prey items were flounder species, and 11.9% of these could be identified as European flounder. Freshwater bream (25.4%) and pike (8.5%) were the second and third most commonly delivered species. The three most commonly delivered prey species at Leiret were freshwater bream (62.7%), pike (12.0%) and perch (10.7%). At Isnes, the three most commonly delivered prey species were freshwater bream (32.4%), perch (27.9%) and common dace (9.9%) (figure 3). In the analysis that included the distribution of the five most common prey species among all prey delivered at the different nests, there was a significant difference in the delivered prey species between the nests ($p<0.0001$)(figure 4).

The estimated average prey body mass ± SE at delivery for all delivered prey items was 228 ± 11 g (ranged 21 g – 805 g) at Elinborg, 181 ± 17 g (ranged 12 g – 528 g) at Huseby, 278 ± 29 g (ranged 7 g – 1171 g) at Isnes, and 452 ± 20 g (ranged 23 g – 1087 g) at Leiret. The analysis of average estimated prey body mass at delivery for all delivered prey items showed a significant difference between the nests ($p<0.0001$). A prey item of average mass at Leiret had a significantly higher body mass compared to prey items of average mass at the other nests (figure 5a). In the analysis of average estimated body mass at delivery for the five most common families among all prey delivered there was also a significant difference between the nests ($p<0.0001$). A prey item of average mass at Isnes had a significantly higher body mass compared to prey items of average mass at Elinborg and Huseby, and a prey item of average mass at Leiret had a significantly higher body mass compared to prey items of average mass at both Elinborg, Huseby and Isnes (figure 5b).

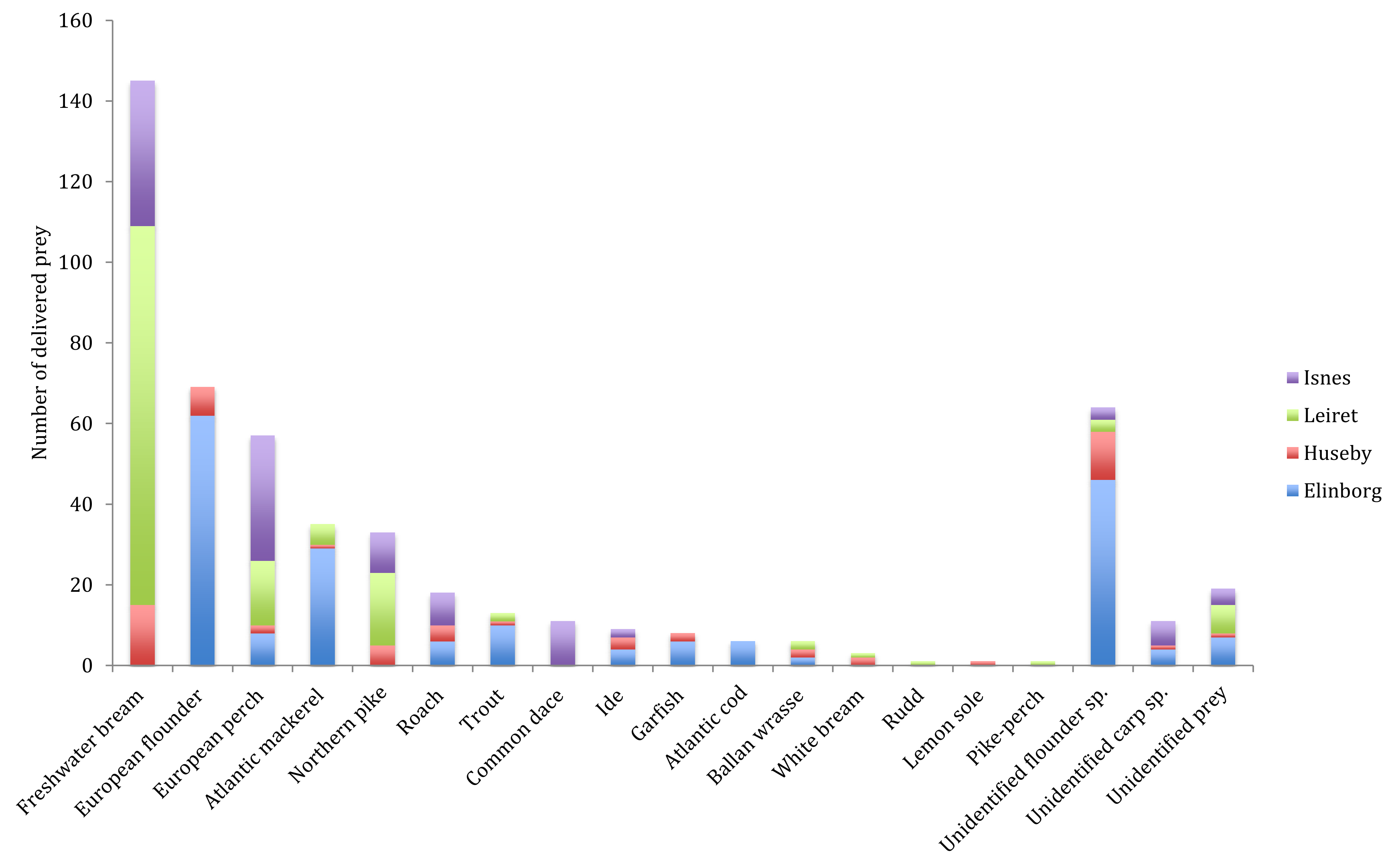


Figure 3: Number of each prey species delivered at the four different osprey nests monitored

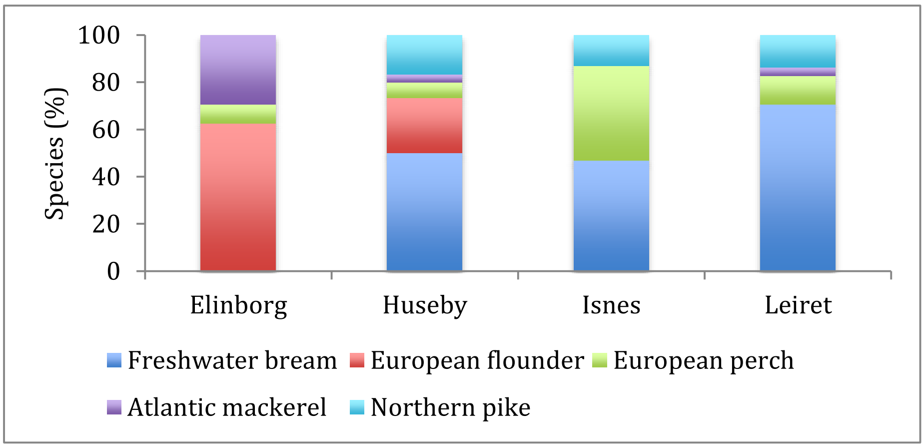


Figure 4: Distribution of the five most common prey species among the prey delivered between the different osprey nests monitored. Whole model: N= 339, df= 12, χ^2= 345.91, p<0.0001.

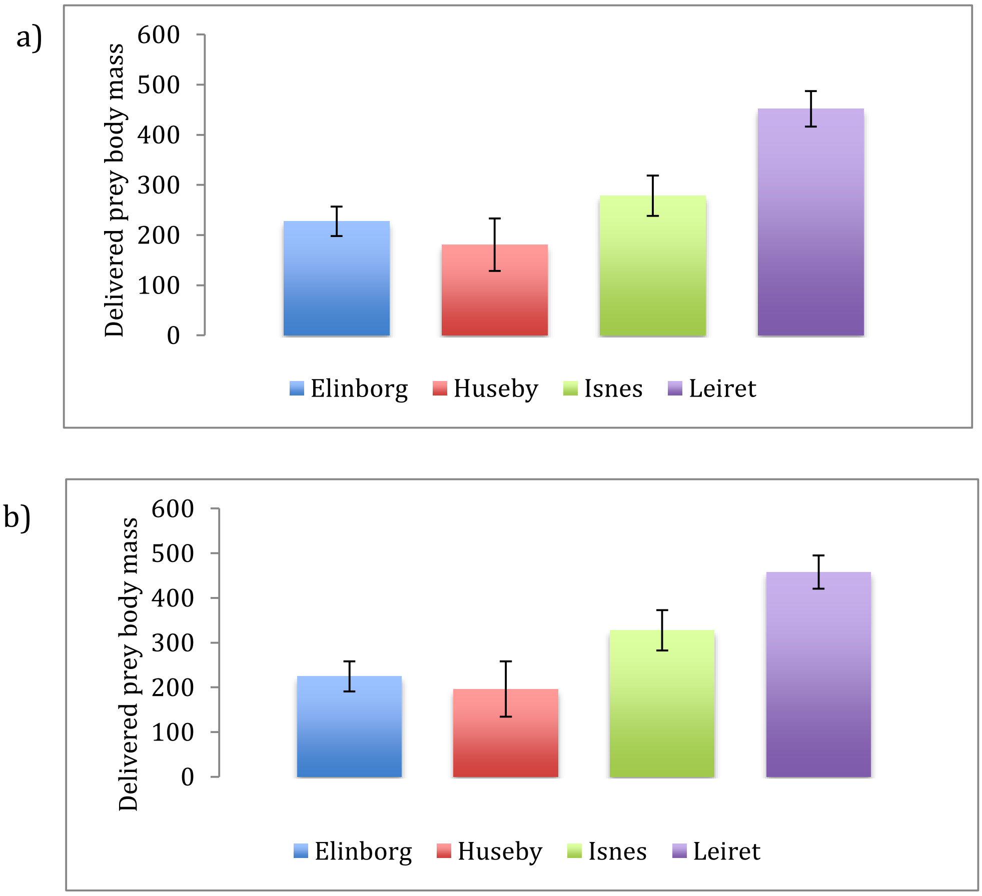


Figure 5: Delivered prey body mass at each of the different osprey nests monitored, based on the analysis for a) all delivered prey items. Whole model: $F_{3, 431}$ = 38.38, p<0.0001, and b) the five most common prey species among all prey delivered. Whole model: $F_{3, 360}$ = 33.41, p<0.0001. The error bars denote 95% confidence intervals.

3.2 Diel activity

Periods of high activity were defined as when the predicted activity curve was above the overall modeled activity curve (MESOR), and periods of low activity were defined as when the predicted activity curve was below the MESOR.

All prey

The mean of the overall modeled activity curve (MESOR) for all delivered prey, i.e. the mean of the predicted probability of at least one prey being delivered within any hour block, was 16.9%. This model (M0) only included the intercept and the nest ID (random effect), and was a poor fit to the data ($\Delta AICc = 193.53$, table 6). The predicted probability of a prey delivery within an hour block was best described by model 3 (table 6), which included the time of day ($p<0.001$) and intercept ($p<0.001$) as fixed effects, and nest ID as random effect (table 7). This model predicted high activity during the entire period between sunrise and sunset (i.e. the period where the predicted activity curve was higher than the MESOR), with a bimodal curve, with two periods where the activity was particularly high. The first peak of particularly high activity was in the hour blocks between 7:00 and 9:00, and the second peak of particularly high activity was in the hour blocks between 17:00 and 19:00 (figure 6).

Table 6: Akaike's information criterion (AICc) model selection of factors that affected the probability of at least one prey item being delivered at an osprey nest within an hour block. See table 2 for model specifications. See table 2 for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
6	9	2326.49	0.00	0.28
18	10	2327.09	0.60	0.21
3	8	2327.79	1.29	0.15
9	9	2327.87	1.38	0.14
21	10	2328.48	1.99	0.10
12	9	2329.74	3.25	0.05
15	10	2329.86	3.37	0.05
5	7	2333.99	7.50	0.01
17	8	2334.62	8.13	0.01
2	6	2335.81	9.32	0.00
8	7	2335.90	9.41	0.00
20	8	2335.93	9.44	0.00
11	7	2337.79	11.30	0.00
14	8	2337.86	11.37	0.00
16	6	2418.43	91.94	0.00
4	5	2418.81	92.31	0.00
7	5	2419.87	93.38	0.00
19	6	2420.81	94.31	0.00
1	4	2420.96	94.47	0.00
13	6	2421.88	95.39	0.00
10	5	2422.71	96.22	0.00
26	4	2498.21	171.72	0.00
24	3	2506.04	179.55	0.00
27	4	2507.49	181.00	0.00
22	3	2507.94	181.44	0.00
25	4	2509.28	182.79	0.00
0	2	2520.02	193.53	0.00
23	3	2521.99	195.50	0.00

Table 7: Effects in model 3 on the predicted probability that at least one prey was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-1.92	0.0850	-22.6	<0.001
I(cos(2 * pi * Hour/24))	-1.21	0.125	-9.68	<0.001
I(sin(2 * pi * Hour/24))	-0.118	0.0740	-1.60	0.11
I(cos(2 * 2 * pi * Hour/24))	-0.908	0.103	-8.80	<0.001
I(sin(2 * 2 * pi * Hour/24))	-0.0300	0.0852	-0.360	0.72
I(cos(3 * 2 * pi * Hour/24))	-0.276	0.0867	-3.19	<0.001
I(sin(3 * 2 * pi * Hour/24))	-0.106	0.0830	-1.27	0.20

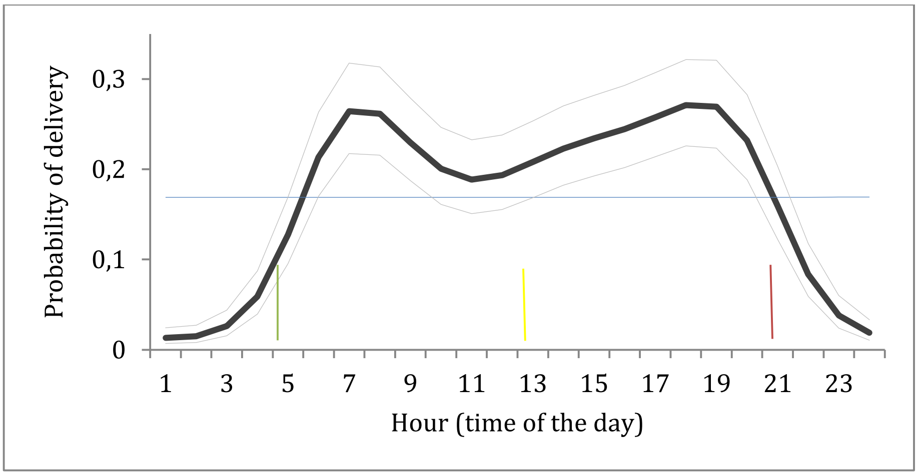


Figure 6: The modeled activity curve describing the predicted probability of at least one prey item being delivered at an osprey nest within an hour block, based on model 3. The horizontal lines denote the model prediction (dark grey), 95% confidence intervals for the model prediction (light grey), and the mean of the overall modeled activity curve (MESOR, blue). The vertical lines denote sunrise (green), solar midday (yellow), and sunset (red) for the average Julian date of the monitoring. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Carps

The mean of the overall modeled activity curve (MESOR) for delivered prey of the carp family was 6.1%. This model (M0) only included the intercept and nest ID (random effect). The predicted probability of a carp being delivered within an hour block was best described by model 3 (Appendix 1, Table I), which included the time of day (p<0.001) and intercept (p<0.001) as fixed effects and nest ID as random effect (Appendix 1, Table VI). The predicted activity curve was bimodal, with the first peak in the hour blocks between 06:00-09:00 and the second peak in the hour blocks between 13:00-20:00 (figure 7).

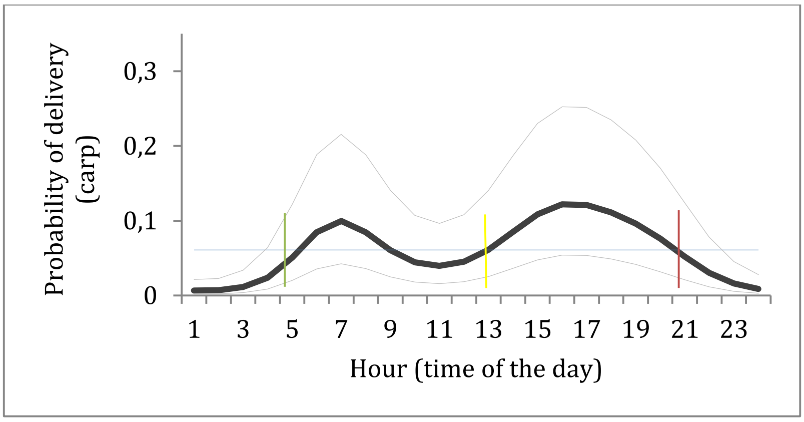


Figure 7: The modeled activity curve describing the predicted probability of at least one prey item of the carp family being delivered at an osprey nest within an hour block, based on model 3. The horizontal lines denote the model prediction (dark grey), 95% confidence intervals for the model prediction (light grey), and the mean of the overall modeled activity curve (MESOR, blue). The vertical lines denote sunrise (green), solar midday (yellow), and sunset (red) for the average Julian date of the monitoring. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Flounders

The mean of the overall modeled activity curve (MESOR) for delivered prey of the flounder family was 1.8%. This model (M0) only included the intercept and nest ID (random effect). The predicted probability of a flounder being delivered within an hour block was best described by model 2 (Appendix 1, table II), which included the time of day (p<0.001) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 1, table VII). This model predicted high activity in the hour blocks between 08:00-20:00. The predicted activity curve was slightly bimodal, with the first peak in the hour blocks between 09:00-12:00 and the second peak in the hour blocks between 16:00-19:00 (figure 8).

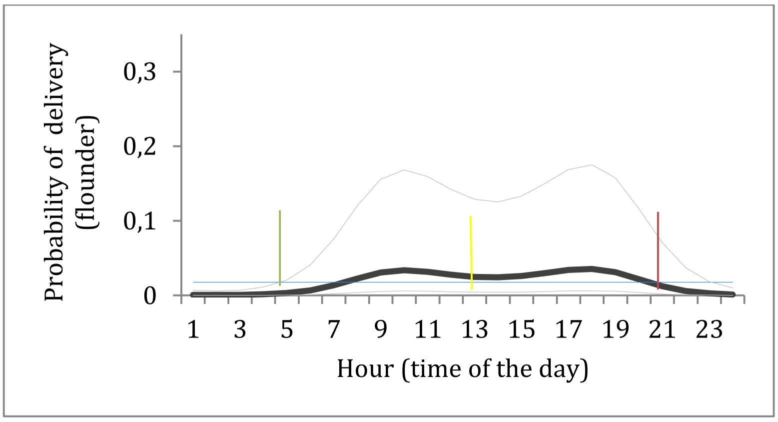


Figure 8: The modeled activity curve describing the predicted probability of at least one prey item of the flounder family being delivered at an osprey nest within an hour block, based on model 2. The horizontal lines denote the model prediction (dark grey), 95% confidence intervals for the model prediction (light grey), and the mean of the overall modeled activity curve (MESOR, blue). The vertical lines denote sunrise (green), solar midday (yellow), and sunset (red) for the average Julian date of the monitoring. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Perches

The mean of the overall modeled activity curve (MESOR) for delivered prey of the perch family was 1.6%. This model (M0) only included the intercept and nest ID (random effect). The predicted probability of a perch being delivered within an hour block was best described by model 2 (Appendix 1, table III), which included the time of day ($p=0.0030$) and intercept ($p<0.001$) as fixed effects, and nest ID as random effect (Appendix 1, table VIII). The predicted activity curve was bimodal, with the first peak in the hour blocks between 06:00-11:00 and the second peak in the hour blocks between 14:00-20:00 (figure 9).

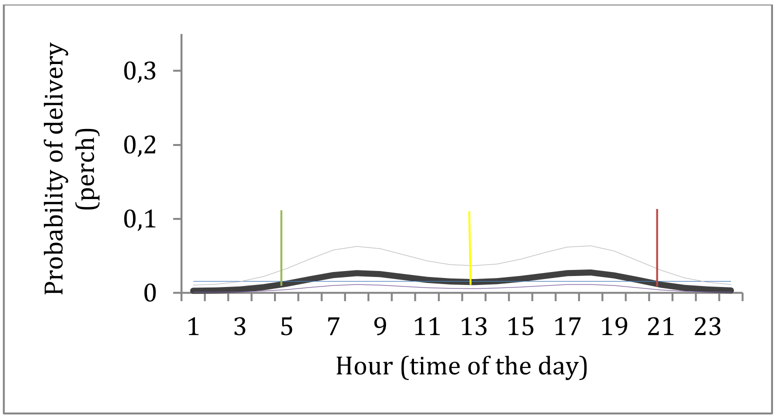


Figure 9: The modeled activity curve describing the predicted probability of at least one prey item of the perch family being delivered at an osprey nest within an hour block, based on model 2. The horizontal lines denote the model prediction (dark grey), 95% confidence intervals for the model prediction (light grey), and the mean of the overall modeled activity curve (MESOR, blue). The vertical lines denote sunrise (green), solar midday (yellow), and sunset (red) for the average Julian date of the monitoring. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Mackerels

The mean of the overall modeled activity curve (MESOR) for delivered prey of the mackerel family was 0.5%. This model (M0) only included the intercept and nest ID (random effect). The predicted probability of a mackerel being delivered within an hour block was best described by model 11 (Appendix 1, table IV), which included the time of day ($p<0.001$), tide ($p<0.001$) and intercept ($p<0.001$) as fixed effects, and nest ID as random effect (Appendix 1, table IX). The predicted activity curve was bimodal with the first peak in the hour blocks between 03:00-10:00 when the lowest astronomical tide (LAT) was below 75 cm, and the second peak in the hour blocks between 16:00-23:00 when LAT was below 55 cm. The modeled activity curve generally showed strongly increasing activity with decreasing tide (figure 10).

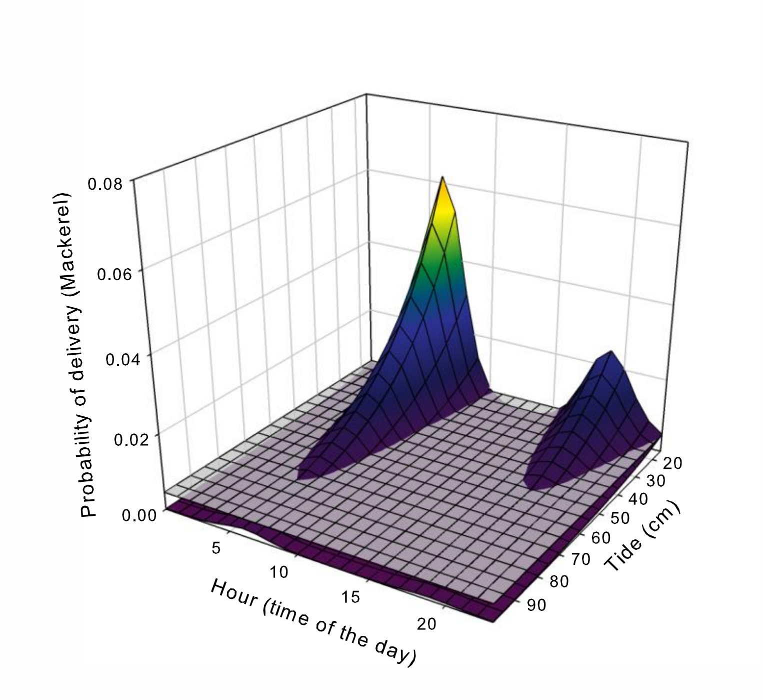


Figure 10: The modeled activity curve describing the predicted probability of at least one prey item of the mackerel family being delivered at an osprey nest within an hour block and at varying levels of lowest astronomical tide (LAT), based on model 10. The grey plane denotes the mean of the overall modeled activity curve. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Model 14 was the second best model (Appendix 1, table IV). This model included the time of day (p<0.001), tide (p=0.0090), wind speed (p=0.074) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 1, table X) i.e. identical to model 11, but with an added effect of wind speed. When taking the minimum registered wind speed (0 m/s) into account, the predicted activity curve was bimodal with the peaks in the same hour blocks as model 11, and a similar trend of increasing probability with decreasing tide. When adjusted for wind, the probability of a prey delivery within an hour block was higher when tide was low, compared with model 11 (figure 11a). When adjusting for average registered wind speed (5.2 m/s), the modeled activity curve showed a similar, but weaker response (figure 11b). At the strongest wind speed registered (18 m/s), the modeled activity curve only showed a very low probability of at least one prey delivery at the nest in the hour blocks between 05:00-07:00 when LAT was below 30 cm (figure 11c).

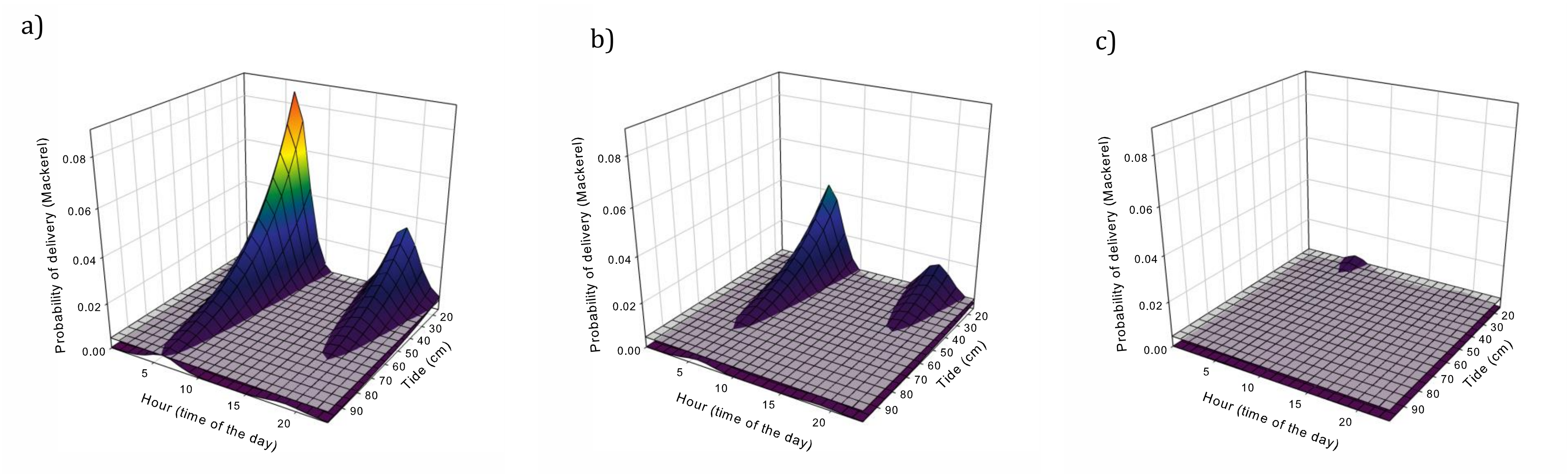


Figure 11: The modeled activity curve describing the predicted probability of at least one prey item of the mackerel family being delivered at an osprey nest within an hour block and at varying levels of lowest astronomical tide (LAT) and wind speed, illustrated by (a) lowest registered wind speed (0 m/s), (b) average registered wind speed (5.2 m/s), and (c) highest registered wind speed (18 m/s), all based on model 13. The grey plane denotes the mean of the overall modeled activity curve. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

Pikes

The mean of the overall modeled activity curve (MESOR) for all delivered prey of the pike family was 0.8%. This model (M0) only included the intercept and nest ID (random effect). The predicted probability of a pike being delivered within an hour block was best described by model 1 (Appendix 1, table V), which included the time of day (p=0.0020) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 1, table XI). The predicted activity curve was unimodal with a peak in the hour blocks between 09:00-19:00 (figure 12).

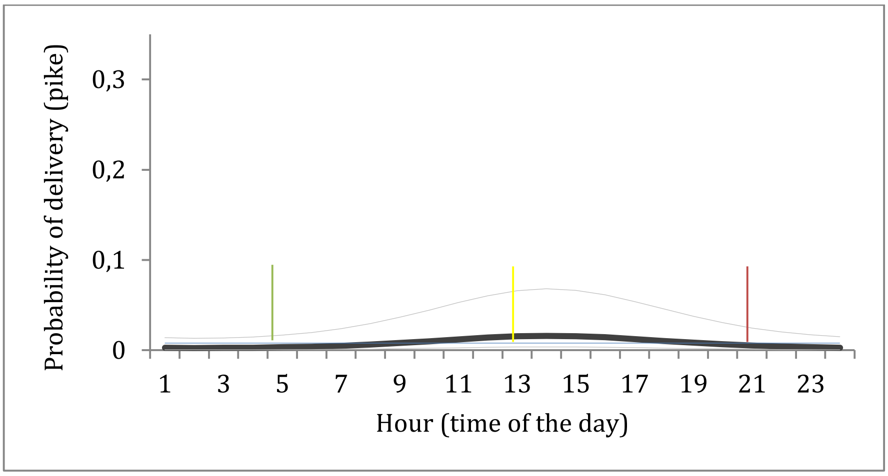


Figure 12: The modeled activity curve describing the predicted probability of at least one prey item of the pike family being delivered at an osprey nest within an hour block, based on model 1. The horizontal lines denote the model prediction (dark grey), 95% confidence intervals for the model prediction (light grey), and the mean of the overall modeled activity curve (MESOR, blue). The vertical lines denote sunrise (green), solar midday (yellow), and sunset (red) for the average Julian date of the monitoring. The probability of a delivery was defined as "high" when the model prediction curve was above the MESOR, and "low" when it was below the MESOR.

3.3 Prey handling at the nest

Feeder

The male delivered 92.3%, while the female delivered 7.7%, of all prey items in the cases where the delivering parent could be determined. The delivering parent could not be scored in 8.6% of the cases. When the nestlings received help dismembering prey items the female provided this help in all cases except one where the assisting parent could be determined, while the feeding parent could not be identified in 9.0% of the cases. The male contributed once at Huseby, when he delivered two prey items at the same time before the nestlings were old enough to feed independently. The female dismembered one of the items in this case, and the male the other.

In the analysis that included the five most common prey families among the prey delivered the predicted probability that the female dismembered the prey rather than the nestlings feeding independently was best described by model 3 (Appendix 2, table I). This model included nestling age ($p<0.001$) and intercept ($p<0.001$) as fixed effects and nest ID as random effect (Appendix 2, table VII). The female was significantly less likely to dismember the prey as the nestlings grew older (figure 13a). The switch, i.e. the point at which the nestlings were predicted to handle 50% of all delivered prey independently, occurred on day 51 after hatching.

In the analysis that included prey body mass for all delivered prey, the predicted probability that the female dismembered the prey rather than the nestlings feeding independently was best described by model 4 (Appendix 2, table II). This model included prey body mass ($p<0.001$), nestling age ($p<0.001$) and intercept ($p<0.001$) as fixed effects, and nest ID as random effect (Appendix 2, table VIII). The female was significantly more likely to dismember larger prey than smaller prey, and at the same time significantly less likely to dismember prey as the nestlings grew older (figure 13b). The switch, i.e. the point at which the nestlings were predicted to handle 50% of all delivered prey independently, occurred on day 39 after hatching for very small prey (<100 g), on day 51 for average sized prey, and on day 63 for large prey (>1000 g).

When comparing the analysis that included the five most common families among prey delivered and the analysis that included prey body mass for all delivered prey, the probability that the female dismembered the prey rather than the nestlings fed independently was best described by model 4 in the latter (Appendix 2, table I and table II)

At Huseby the nestlings died before they started to feed independently. At Elinborg the nestlings were observed to feed independently for the first time at an age of 49 days, at Isnes at an age of 34 days, and at Leiret at an age of 55 days.

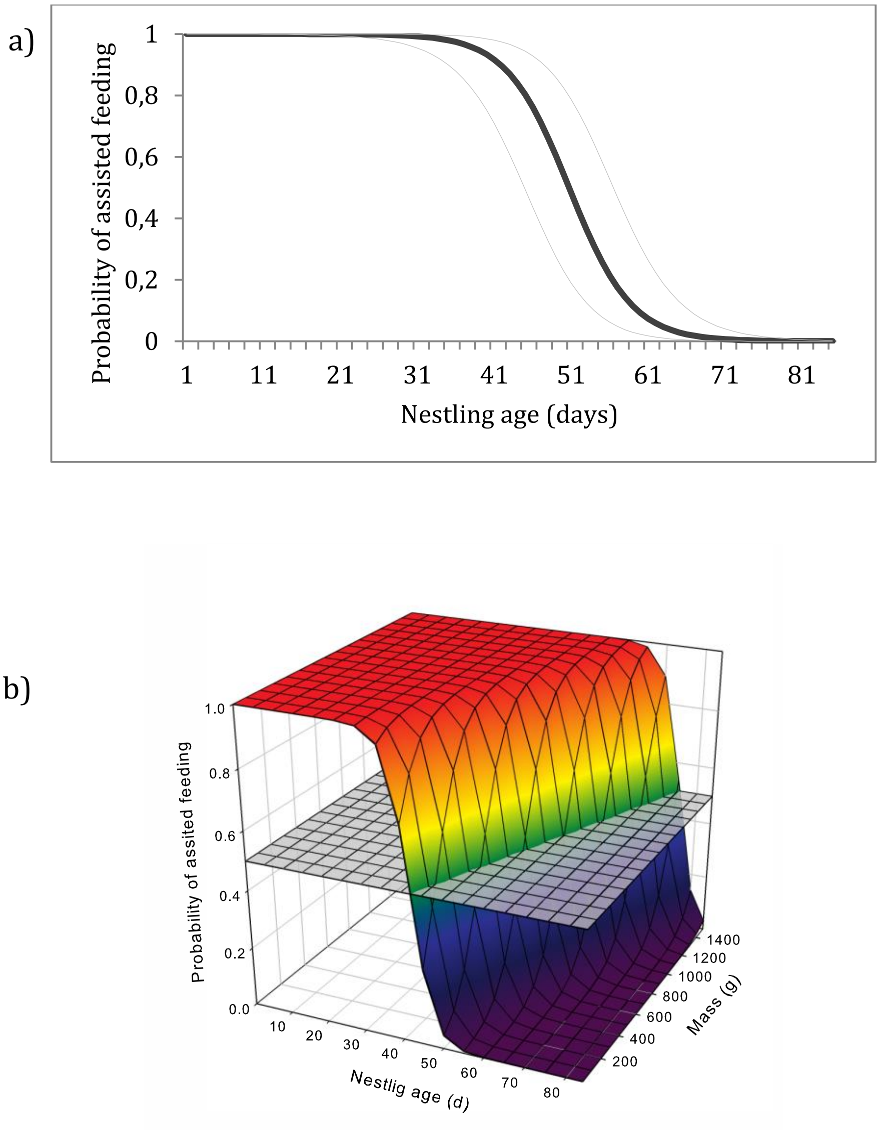


Figure 13: The predicted probability that the osprey female dismembered the delivered prey item rather than the nestlings fed independently, based on a) model 3 in the analysis that included the five most common prey families among all prey delivered as an explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae, and b) model 4 in the analysis including prey body mass for all delivered prey. The horizontal plane shows the level at which the nestlings were equally likely to ingest the prey unassisted as being fed by the female.

Partial prey consumption prior to delivery

More than just the head had been removed, and presumably eaten, prior to delivery at the nest for almost half of the prey items (49.1%). Whether or not a prey item had been eaten at could not be scored in 5.3% of the cases.

In the analysis that included the five most common prey families among all prey delivered, the predicted probability that a prey item had been eaten at prior to delivery was best described by model 2 (Appendix 2, table III). This model included the five most common prey families; Cyprinidae (reference), Esocidae ($p=0.42$), Percidae ($p<0.001$), Pleuronectidae ($p=0.24$), Scombridae ($p=0.016$) and intercept ($p=0.72$) as fixed effects, and nest ID as random effect (Appendix 2, table IX). Perches were significantly less likely to be eaten at prior to delivery compared with cyprinids, while mackerels were significantly more likely to be eaten at. For the other prey families there was no significant effect (figure 14).

In the other analysis, including prey body mass for all delivered prey as an explanatory variable, the predicted probability that the delivered prey had been eaten at when delivered at the nest was best described by model 2 (Appendix 2, table IV). This model included prey body mass ($p=0.89$) and intercept ($p=0.44$) as fixed effects and nest ID as random effect (Appendix 2, table X). Hence, prey mass did not explain the variation in the model significantly.

When comparing the analysis that included the five most common delivered prey families and the analysis that included prey body mass for all delivered prey, the probability that the delivered prey had been eaten at was best described by model 2 in the former (Appendix 2, table III and table IV).

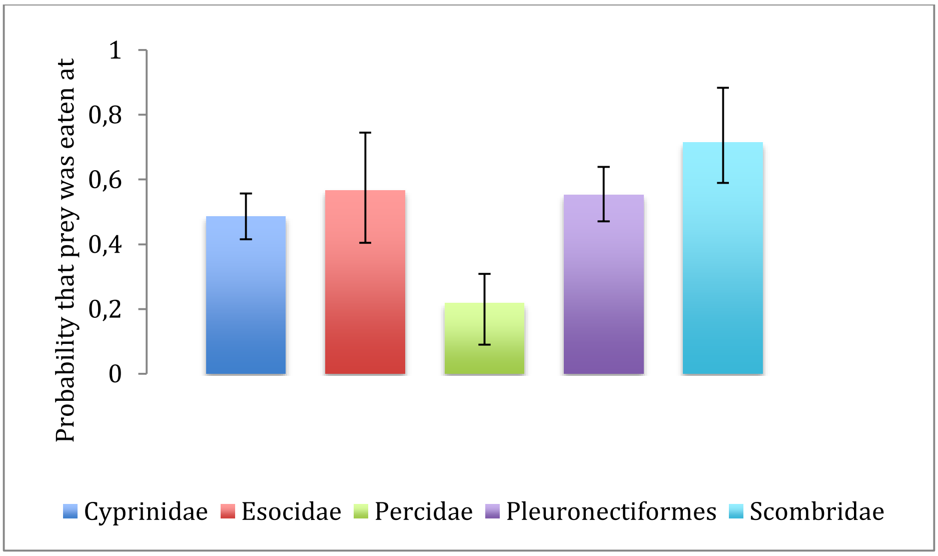


Figure 14: The probability that a prey item delivered at an osprey nest had been eaten at prior to delivery, based on the analysis including "prey family" for the five most common prey families among all prey delivered as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. Cyprinidae is the reference level in the analysis. The error bars denote 95% confidence intervals.

Decapitated prey prior to delivery

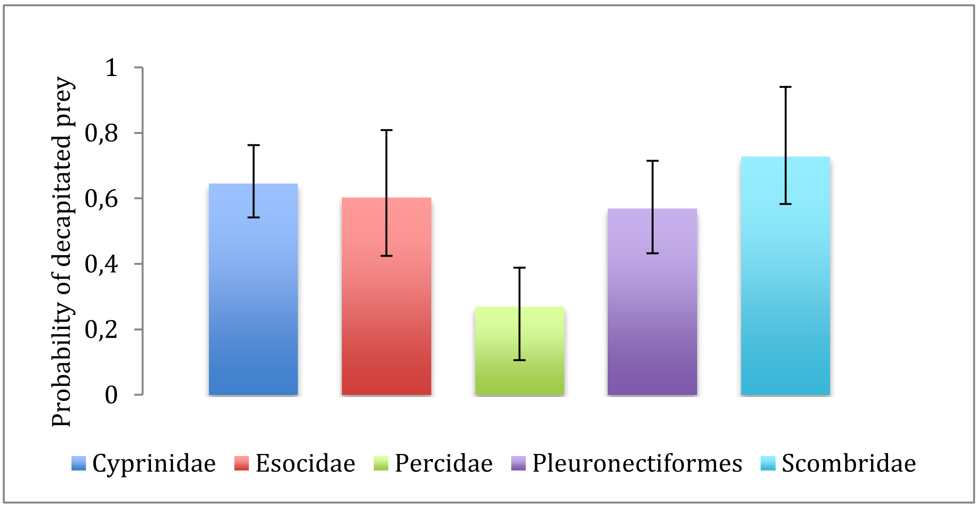
Of all the prey items delivered, 9.9% had been decapitated prior to delivery, but not more eaten at. Whether or not a prey item was decapitated could not be scored in 5.3% of the cases.

In the analysis that included the five most common prey families among all prey delivered the predicted probability that a prey item had been decapitated prior to delivery was best described by model 2 (Appendix 2, table V). This model included the five most common prey families; Cyprinidae (reference), Esocidae (p=0.65), Percidae (p<0.001), Pleuronectidae (p=0.32), Scombridae (p=0.43) and intercept (p=0.017) as fixed effects, and nest ID as random effect (Appendix 2, table XI). The model showed that perches were significantly less likely to be decapitated prior to delivery compared with cyprinids, while for the other prey families there was no significant effect (figure 15a).

In the other analysis, including prey body mass for all delivered prey items as an explanatory variable, the predicted probability that the delivered prey was decapitated was best described by model 2 (Appendix 2, table VI). This model included prey body mass ($p<0.001$) and intercept ($p=0.31$) as fixed effects, and nest ID as random effect (Appendix 2, table XII). The model showed that the probability of decapitation increased significantly as prey mass increased (figure 15b).

When comparing the analysis that included the five most common delivered prey families among all prey delivered and the analysis that included prey body mass for all delivered prey, the probability that the delivered prey had been decapitated prior to delivery was best described by model 2 in the former (Appendix 2, table V and table VI).

a)



b)

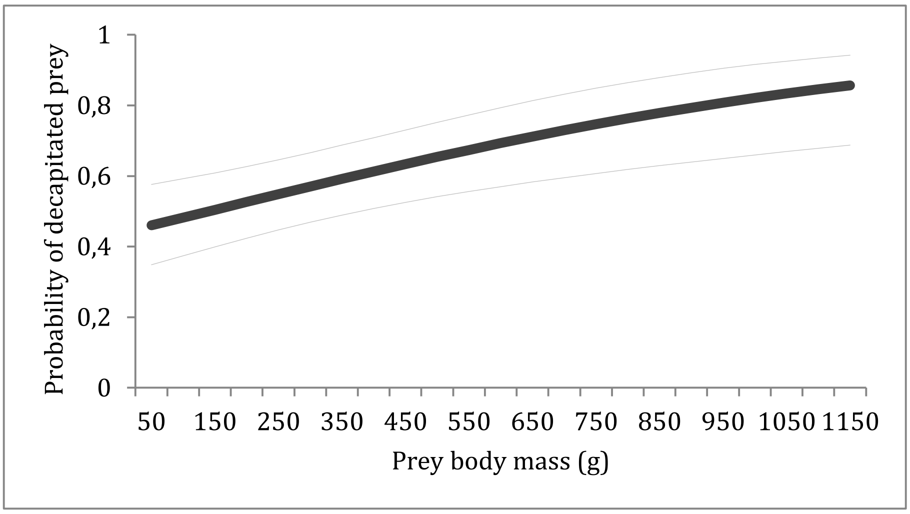


Figure 15: Probability that a prey item delivered at an osprey nest had been decapitated prior to delivery, based on a) model 2 in the analysis including "prey family" for the five most common prey families among all prey delivered as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. The error bars denote 95% confidence intervals. b) model 2 in the analysis including prey body mass for all delivered prey items. The horizontal lines denote the model prediction (dark grey) with 95% confidence intervals (light grey).

3.4 Feeding effort

The predicted mass of prey received at the nest per nestling per monitored hour block during the entire breeding season was best described by model 2 (Appendix 3, table I), which was a linear model including Julian date (p=0.078) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 3, table II). The model showed a marginally non-significant and weak decrease in the mass of prey received at the nest during the entire breeding season (figure 16).

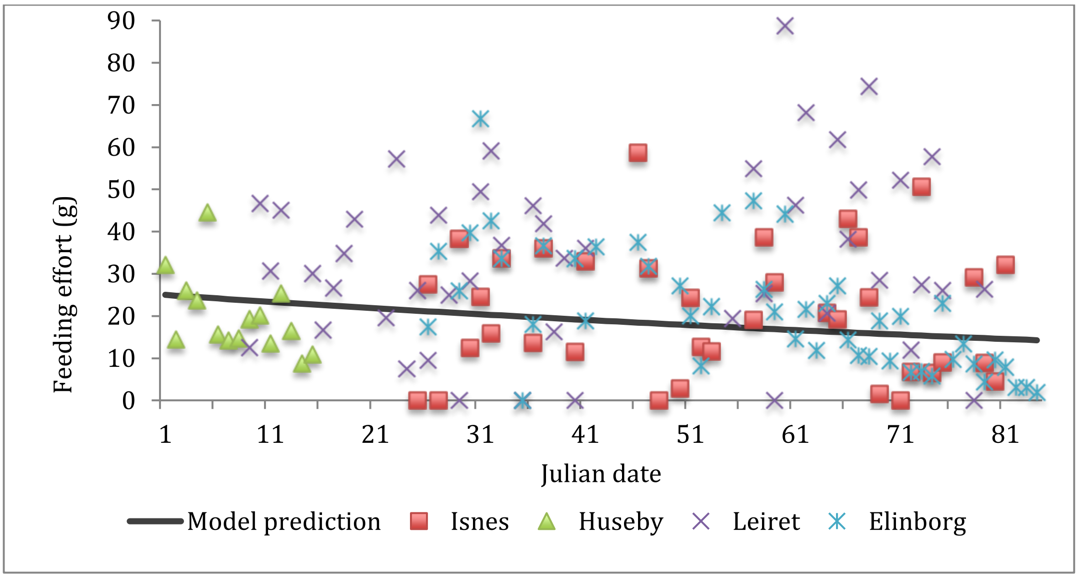


Figure 16: Estimated feeding effort, i.e. the mass of prey each osprey nestling received at the nest per monitored hour block throughout the nestling period. Note that the model was not corrected for the mass of food eaten by the female at the nest.

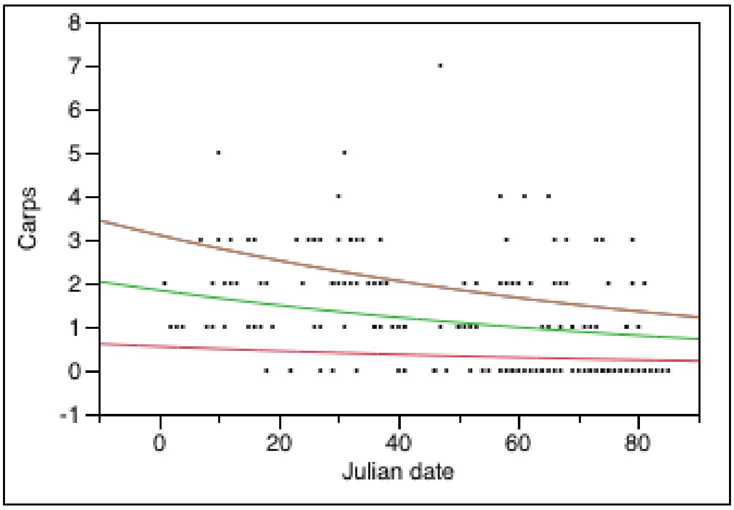
The mass of prey received at the nest per nestling per monitored hour block before the first nestling fledged was best described by model 1 (Appendix 3, table II), which was a linear model including nestling age (p=0.65) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 3, table III). The model showed a very weak increase in the amount of prey received per nestling before the first nestling fledged, but the effect of nestling age was far from being significant.

Model 2 was the second best model describing the mass of prey received at the nest per monitored hour block before the first nestling fledged (Appendix 3, table II), a linear model that included Julian date (p=0.92) and intercept (p<0.001) as fixed effects, and nest ID as random effect (Appendix 3, table V). This model also showed a very weak increase in the amount of prey received per nestling before the first nestling fledged, but the effect of Julian date was far from significant.

Seasonal distribution of prey items

Carps were delivered at the nests throughout the nestling season, with a significant decrease in the daily number of prey item deliveries (p= 0.0034) (figure 17a, Appendix 4, table I). Flounders were also delivered from the beginning of the nestling season, but with a non-significant change in the daily number of deliveries throughout the nestling season (p= 0.89) (figure 17b, Appendix 4, table II). The first perch was delivered on day eight, and the daily number of deliveries showed a marginally non-significant decrease throughout the nestling season (p= 0.058) (figure 17c, Appendix 4, table III). Mackerel was delivered for the first time on day 15, with a non-significant change in the daily number of deliveries throughout the nestling season (p= 0.79) (figure 17d, Appendix 4, table IV). Pike was initially delivered on day 8, and the daily number of deliveries showed a significant decrease throughout the nestling season (p= 0.0096) (figure 17e, Appendix 4, table V).

a)


Carps
8
7
6
5
4
3
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1
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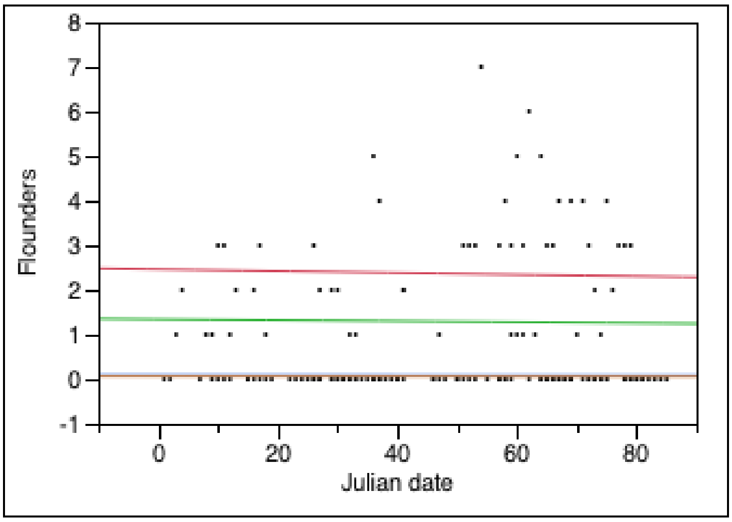
40
60
80
Julian date

b)


Flounders
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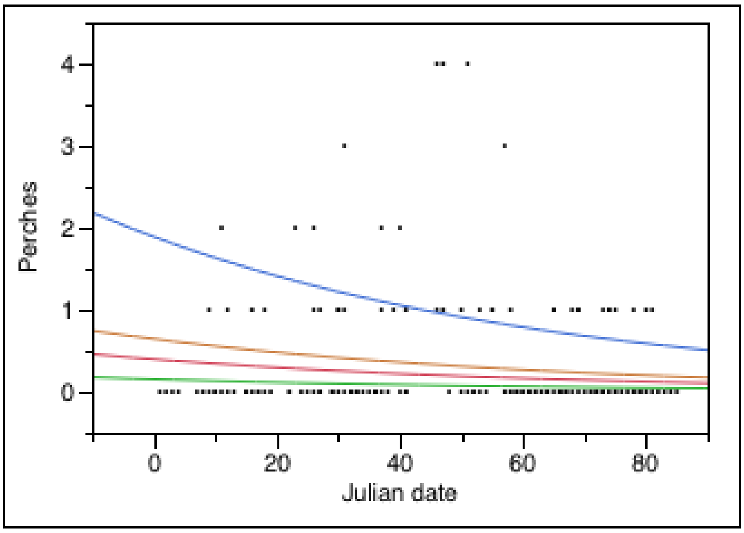
80
Julian date

c)


Perches
4
3
2
1
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Julian date

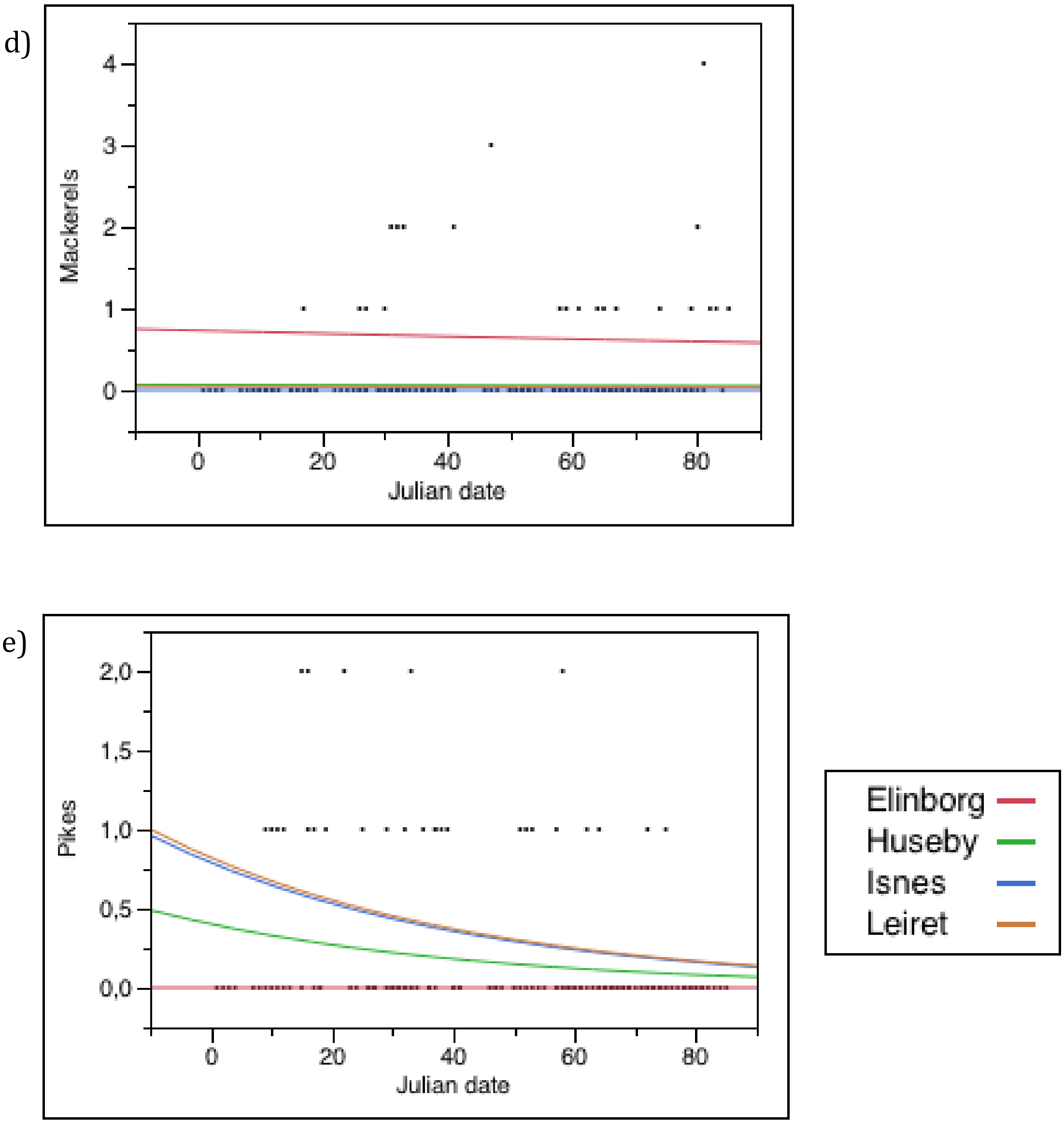

Figure 17: Seasonal distribution of the number of prey items delivered at each of the osprey nests monitored per day for the five most commonly delivered prey species, a) carps, whole model: N= 198, df= 3, χ^2= 8.59, p= 0.0034, b) flounders, whole model: N= 134, df= 3, χ^2= 0.0195, p= 0.89, c) perches, whole model: N= 58, df= 3, χ^2= 3.60, p= 0.058, d) mackerels, whole model: N= 35, df= 3, χ^2= 0.0729, p= 0.79, and e) pikes, whole model: N= 33, df= 3, χ^2= 6.71, p= 0.0096. The tests were corrected for nest ID. Julian date 1 was set to 1 June

4 Discussion

4.1 Prey selection

In total, I found that cyprinids were the most important prey at the four osprey nests. At species level, freshwater bream was the most important prey with 48.6% of the estimated total delivered body mass. European flounder, European perch, mackerel and pike were also important prey species at the nests. These species contributed to the estimated total delivered prey body mass with 12.0%, 9.7%, 5.2% and 5.8%, respectively. Nordbakke (1974, 1980) found that freshwater bream only accounted for 5.3% of the total estimated weight of all the prey he recorded, although the freshwater bream was recorded as present in his study area. Hagen (1952), Schnurre (1956, 1961), and Häkkinen (1978), on the other hand, found that freshwater bream was the most commonly delivered prey species at osprey nests in areas of Norway, Germany and Finland, respectively. In Nordbakke's study, European flounder, which was recorded as present in the study area, only contributed to 1.7% of the total estimated prey body mass, and mackerels were not registered at all. In my study, ide only contributed to 1.9% of the total estimated delivered prey body mass, while in Nordbakke (1974, 1980) ide was the most important prey species with 51.4% of the total estimated prey body mass. Pike and perch were among the most important prey species in both Häkkinen's (1978) and Nordbakke's studies (1974, 1980), which correspond well with my findings.

Spanish mackerels (*Scomberomorus maculatus*) have been registered as prey for the osprey in Chesapeake Bay on the American east coast (McLean & Byrd 1991), but to the best of my knowledge, Atlantic mackerels have not earlier been registered as prey in Scandinavia. Parts of Nordbakke's study (1974, 1980) took place approximately 8 km from the coast. Hence, marine hunting sites were within reach, even though freshwater lakes were closer. The Dyfi Osprey Project (2013) in the UK informs on their public web site that their monitored ospreys have started catching mackerels in recent years, where they earlier did not.

However, to the best of my knowledge, this has not yet been confirmed in any scientific publications.

The discrepancies between earlier findings and mine may be due to differences in availability of the different fish species between the different study areas, even though my, Hagen's (1952) and Nordbakke's (1974, 1980) study areas are in the same region of Norway. The different prey species are only documented as "present" or "not present" at each freshwater site in the map (Turkart Østfold 2016), but this is not a scientific database. To the best of my knowledge, numerical and spatial distributions of each species are unknown, both for the ecosystems in the 1950s, 1970s and today. If the ospreys are opportunistic foragers, as my study and prior diet studies indicate (Hagen 1952, Nordbakke 1974, 1980, Häkkinen 1978, McLean & Byrd 1991), the ospreys will catch more of the fish species that have a higher relative availability, compared to species with lower relative availability, simply because the chance of spotting and capturing a more available prey is larger than spotting and catching one that is less available, and thus reduce the costs associated with searching time (Stephens & Krebs 1986). By available I mean not only a species of high abundance, it also has to be accessible in the sense of visibility and vertical distribution in the water. Thus, local variations in numerical and spatial species distributions and changes in these distributions through time may be the reason for the variation observed between the different studies in this case.

Mackerel was not an expected prey type, primarily because I did not find any reports of ospreys preying on this species in the research I did before the study started. Furthermore, the mackerel is a very fast and vigorous fish, and one would think this makes it difficult for the osprey to capture. On the other hand, the mackerel is diurnal and swim in large schools close to the surface, which are factors that make it possible for the osprey to spot the fish from the air, and dive down to capture it (Cramp & Simmons 1979). As for the other prey species, relative availability may be an important factor. The mackerel population in the North Sea experienced a drastic decline in the 1960-1970s due to overexploitation (Iversen 2002). Studies indicate that the mackerel population has expanded, both in number and geographic distribution, over the last 10-15 years (ICES 2013, Berge et al. 2015). The lack of mackerels in the diet in this area in 1972-73 may simply be due to the fact that there were very few mackerels to be caught, while today's distribution makes it a favorable prey for ospreys that have access to the coast.

I found that the average estimated body mass of prey caught was 380 g, while the average estimated prey body mass delivered at the nest was 293 g. Nordbakke (1974, 1980) reported an average estimated prey mass of 200-300 g based on his analysis of prey remains, while Häkkinen (1978) reported an average estimated prey mass of 150-350 g, i.e. somewhat lower than my findings. Again, if the osprey forages opportunistically, these differences may be caused by differences in prey availability and changes in size distribution within a prey species population over time and between different prey populations. The freshwater bream is also generally larger and heavier than the ide (Kottelat & Freyhof 2007), thus the difference in the most important prey type between the study of Nordbakke (1974, 1980) and mine may contribute to a higher average estimated mass in my case. Individual differences between ospreys in a population may also cause variation between different nests in estimated body mass of prey delivered, as documented both in my study and that of Nordbakke (1974, 1980), together with differences in prey availability at each nest site.

Both video recording and prey remain analyses used for estimation of prey body mass are prone to inaccuracies. In my case, prey delivered at the nest were probably not as heavy as reported due to many items being decapitated prior to delivery, because heads are relatively heavy compared to the rest of the body. Analyses of prey remains in both the osprey (Häkkinen 1978) and other raptor species have probably resulted in an underestimation in the number of small prey, because they leave less remains than larger prey (Slagsvold et al. 2010). Thus, the estimates made by Nordbakke (1974, 1980) are probably also too high. I argue that video monitoring is a more accurate method for both prey species determination and prey mass estimation, since all delivered prey are registered as long as the camera is running and the visibility is satisfactory. Video monitoring also causes less stress for the studied individuals, since one does not have to visit the nests, but can operate the camera equipment from a distance.

Differences in delivered prey species between the nests

Type of prey delivered at Elinborg differed from type of prey delivered at the other nests. The three most important prey species at the Elinborg nest, which was the one closest to the sea, were all saltwater species, while both salt – and freshwater species contributed to the main diet at Huseby. At Leiret and Isnes, which were furthest away from the sea, the three most important prey types were all freshwater species. It seems like the proportion of salt – and freshwater species in the diet is a direct response of the distance to a salt – or freshwater fishing locality.

It is reasonable to assume that the osprey takes the distance to the different fishing sites into account when deciding where to go to search for prey, as predicted by optimal foraging theory (Stephens & Krebs 1986, and references therein). Hunting relatively close to the nest is favorable in order to minimize time and energy costs used when flying to and from the fishing locality, given that favorable prey are available at the locality in question, compared with flying further away to catch a prey of similar energetic value. Such a strategy will maximize the net energy gained per time unit. This may explain the differences in prey composition between the different nest sites, since the different osprey nests studied were located close to different potential fishing sites, with a corresponding potential variation in prey species availability. Even though they were closer to the sea, the ospreys at Elinborg did however occasionally deliver freshwater species at the nest. Similarly, the ospreys at Leiret delivered a few saltwater species at the nest, even though the sea was far away compared to the closest freshwater fishing site. Especially the two wrasses delivered at the latter nest were caught on a day with heavy rain, while the freshwater species at Elinborg seemed to be delivered at a time when the tide was high. The osprey may have acquired experience about how different factors like these change the availability of prey at its more frequently visited fishing site at certain periods, making it more profitable to fish somewhere else, even though time – and energy costs used for transport are higher.

The average estimated prey body mass delivered at Leiret was higher than the average estimated prey body mass delivered at the other nests, both in the analysis including prey body mass for all delivered prey items and in the analysis including only prey body mass for the five most common families among all prey delivered. In the latter analysis, prey items delivered at Leiret were also heavier than prey items delivered at Huseby and Elinborg. These differences may be caused by differences in prey availability between the nest sites. As mentioned above, the freshwater bream is also generally a large fish compared to many other fish species (Kottelat & Freyhof 2007). That may have contributed to the high average estimated body masses at Leiret and Isnes, where the freshwater bream was frequently delivered throughout the nestling season.

4.2 Diel activity

All prey

The time of day was the model with the best fit in the diel activity analysis for all prey, and predicted a period of high activity throughout the entire day between sunrise and sunset, with especially high activity between 07:00-09:00 and 17:00-19:00. Dennis (2008) has observed a similar activity pattern in the osprey population in Scotland.

A pattern of high activity during the daylight hours was expected, since the osprey depends on spotting a fish from the air, before plunging into the water and catching it with its talons (Cramp & Simmons 1979). The early peak of particularly high activity may be due to a need for energy after hours with no prey deliveries during the dark night hours. Likewise, the peak of particularly high activity in the evening may be due to a renewed demand for energy after the early morning peak, and a need to fill the energy reserves before it gets dark, preventing the osprey male from hunting, in order to avoid starvation (Davies et al. 2012). Generally cooler temperatures at night, making it more energy consuming to keep the body temperature up, might reinforce the need for food at these times of the day. Norwegian summer nights are short, however, and the time passing between two deliveries during the day are not necessarily any shorter than the time passing between the last delivery at night and first delivery the next morning (pers. obs.).

An additional factor is that the hunting behavior of the osprey may not only be a result of its own ecological and physiological activity pattern, but also determined by the activity patterns of its prey, or possibly a combination of the two (Erkert & Kappeler 2004). According to Reebs (2003), fish in general tend to be very plastic in relation to activity patterns, and some individuals may even change their activity pattern from diurnal to nocturnal in a few days. Taken into account that the osprey is capable of feeding upon a range of different fish species, and the interspecific variation and intraspecific plasticity in activity patterns of potential prey, one would think that the osprey should be able to capture suitable prey at any time during the light of day. Thus, it seems more likely that the observed activity pattern of deliveries of all prey types is caused primarily by the osprey behavior itself, and not the activity patterns of all the different types of fish.

Carps

The model including the time of day was the best fit to explain the activity pattern of carp deliveries at the nest. There was a high probability of delivery of carps at the nest compared with other prey species, and the activity peaked in the hour blocks between 06:00-09:00 and 13:00-20:00. Thus, the predicted activity curve of carp deliveries fits well with the overall predicted activity of deliveries in the osprey, which is as anticipated, considering that carp species contributed to almost half of all delivered prey species at the nests. To the best of my knowledge, no other studies have looked into the activity patterns of the osprey in connection with specific prey types. The freshwater bream, which constitutes most of the prey items in the carp family in this study, often swim in shoals (Kottelat & Freyhof 2007) and has been shown to migrate from offshore areas to inshore areas and to the upper water layers during the night (Vasek & Kubecka 2004, Lyons & Lucas 2002). Alabaster & Robertson (1961) also report an increased level of activity at dawn and dusk.

Since the osprey rarely dives deeper than 1 m when fishing (Cramp & Simmons 1979), the vertical distribution of freshwater bream during the night and early morning makes it more accessible during these hours. Poor light during the middle of the night will however limit the osprey's ability to spot and capture prey in the water. It may seem like both the ospreys' dependence on daylight, their need for energy in the morning and the carps' distribution during the early morning hours contribute to making them such a common prey at this time of the day. The second peak of activity is also within the daylight hours, making light conditions preferable for the osprey. However, one would think that the distribution of freshwater bream in deeper waters during this time of the day makes them hard for the ospreys to catch. One possible explanation is that some freshwater breams occur in shallow waters during parts of the day, where the water is warmer (Froese & Pauly 2016b, and references therein), and the ospreys are capable of capturing them.

Flounders

The probability of a flounder being delivered at a nest was best described by a model including the time of day. The predicted probability of a delivery was high in the hour blocks between 08:00-20:00, with two peaks of particularly high activity in the hour blocks between 09:00-12:00 and 16:00-19:00. Observations from Dennis (2008) claim that flounders are most commonly captured by Scottish ospreys when the tide is low, and thus occupy shallow waters. However, the models including tide did not affect the probability of a flounder being delivered in my study. Studies of flounder behavior have shown that flounders have certain movement patterns in relation to the tidal cycle (Wirjoatmodjo & Pitcher 1984, Gibson 1997) and light conditions (Gibson 1997).

When taking studies on flounder behavior into account, one should expect tide to have a stronger effect on prey deliveries at the nest than what I found. One possible explanation is that the European flounder constitutes a large proportion of all delivered flounder species in my study, and that the majority of the unidentified flounders probably also belong to this species. The European flounder is capable of living in brackish water (Froese & Pauly 2016c), which is available in the lower parts of the river Glomma. In this area the tidal cycle is less evident than along the coast. The flounders may therefore stay approximately in the same area despite of the tidal cycle, in fairly shallow waters where the osprey is able to spot and capture them during the daylight hours. Thus, the activity pattern of flounder deliveries at the nest seems to be determined both by the ospreys' general diurnal behavior and by the lack of horizontal movements in the flounders.

Perches

For deliveries of prey items from the perch family a model including the time of day was the best fit, with a high predicted probability of prey delivery in the hour blocks between 06:00-11:00 and in the hour blocks between 14:00-20:00. European perch, which constituted most of the deliveries in the perch family, were most active during daytime and spent approximately the same amount of time in the upper and lower water levels in a laboratory study at the Arctic Circle in Sweden (Eriksson 1978). In Finland perch seem to be diurnal, but with a slight decrease in activity during the time of solar midday (Rask 1986). The latter study also found periodic switches to higher activity at dawn and dusk, depending on what prey the perch fed on at a given time or at a given size.

The periodic vertical distribution in upper water masses would make the perch available as prey for the osprey. The diurnal activity pattern of both the perch and the osprey fit well together. The decrease in activity of both species around solar midday may indicate that the activity of the perch at least partly contributes to the activity pattern observed in my study, even though a similar trend can be seen in the activity pattern for several of the prey species in general.

Mackerels

For mackerels the model including the time of day and the level of lowest astronomical tide (LAT) had the best fit. Additionally, the second best model included wind speed. There was a high probability of a mackerel being delivered at the nest in the hour blocks between 03:00-10:00 and 16:00-23:00, but the probability decreased drastically at higher tide and stronger wind. Mackerels forage in large schools in the upper water masses close to the coast as the water warms up during the summer (Froese & Pauly 2016d). In Canada, Atlantic mackerels had a greater stomach fullness during the day compared with the night, and a peak around mid-afternoon, indicating that they foraged more actively at this time of the day (Darbyson et al. 2003).

When taking only tide and the time of day into consideration one would expect the mackerels to be most available to the osprey during the afternoon on days with low tide at this time of day, when they are most active and vertically distributed in such a way that the osprey can spot them from the air and plunge down to capture them. However, this is not the case in my analysis. Weak wind is obviously crucial for the osprey to be able to capture mackerels. Grubb (1977) claims that wind speed in itself did not affect the rate of successful dives in ospreys, but that water surface conditions did, so that a rippled surface decreased the rate of successful dives. It is reasonable to believe that these two variables often are closely correlated, especially along the coast, where there is little shelter from the wind. Due to sea breeze caused by the uneven heating during daytime between land and the adjacent water, the wind speed is generally known to increase during the middle of the day, and decrease or turn around, i.e. land breeze, towards the night (Ackerman n.d.). Thus, the water surface is probably smoother during morning and evening, compared to during the rest of the day, making it possible for the osprey to spot and capture mackerel at these times of the day. The phenomenon of uneven heating between land and the adjacent water applies to all bodies of water, but the freshwater lakes in my study area are too small to give any notable effect.

The osprey's dependence on little wind is of concern, considering that global climate changes are predicted to induce more frequent and stronger winds in the future (IPCC 2007). Especially for ospreys along the coast, feeding mainly on marine prey species such as the mackerel, increasing wind speed may dramatically reduce their ability to capture prey close to the nest. It will then become less favorable to breed along the coast, and I would expect ospreys in my study area to settle inland, where they can fish more easily in freshwater lakes and rivers. The number of occupied osprey nests along the coast in my study area as well as the number of pairs with documented breeding success through fledging juveniles has declined during recent years (O. J. Hanssen pers. comm.), increasing the concern that some osprey populations at the coast line may be vulnerable to climate change.

Pikes

The diel pattern of pike deliveries at the nest was best explained by a model including the time of day, and showed a period of high activity in the hour blocks between 09:00-19:00, with the top of the peak occurring around solar midday. Jepsen et al. (2001) found no pattern in the diel activity of pikes during the summer season in Denmark. Beaumont et al. (2005), on the other hand, found a peak in activity of pikes around dawn and dusk in England. They also observed some intraspecific variation, where certain individuals tended to be more crepuscular.

According to the activity patterns of pikes described above I would expect pike deliveries at the nest to either be equally probable throughout the day, or show periods of high activity around dawn and dusk, when the prey species is assumingly most active. The former pattern is reflected in my analysis. The pike is however the only prey species with a slight increase in the probability of being delivered around solar midday, whereas for the other four most commonly delivered prey types there was a slight dip in the probability of delivery during the middle of the day. Assuming that the osprey is an opportunistic hunter, pikes might be relatively more available to the osprey at this time compared with other types of prey, and therefore be more frequently delivered at the osprey nests around solar midday. Alternatively, other prey types may generally be more available at other times of the day, and therefore the pike is delivered less frequently then.

Another possible reason is that the patterns of deliveries of each prey type vary due to factors not taken into account in my analyses, such as cloud cover, precipitation, wind direction and distance to specific fishing grounds. Coincidences in the data set may also give random effects in the modeling, which do not reflect an actual biological response.

4.3 Prey handling

Feeder

The predicted probability that the female dismembered the prey rather than the nestlings ingested prey unassisted was best described by nestling age and prey body mass. The females at the different nests fed their nestlings all types of prey for an average period of 46 days. According to the model prediction, the nestlings were equally probable to feed unassisted as assisted on prey items of average body mass after 51 days, and they fed unassisted on smaller prey items earlier than larger prey items. This switch is late compared with other raptor species feeding at least partly on vertebrates, such as the Eurasian kestrel, Ural owl and the golden eagle (Sonerud et al. 2014a,b, Dihle 2015, Nygård 2015), but the general pattern that the probability of independent feeding increased with nestling age and decreased with increasing prey body mass corresponds well with earlier studies (Steen et al. 2010, Sonerud et al. 2014a,b). Larger prey items were probably harder for the nestlings to handle, due to a rougher and thicker surface, and larger bone structures that are hard to tear off, as well as difficult to swallow.

When observing the video recordings it did however seem like the females continued to feed the nestlings longer than necessary, when it looked like they had acquired the skills to handle the prey items themselves. The females often grabbed the prey item forcefully from the males, or even from the nestlings. This can be interpreted as a family conflict between a female and her nestlings, where the female attempted to reduce her foraging costs and maximize her future potential fitness by exploiting a resource primarily meant for her young (Sonerud et al. 2013). At the same time, it was crucial that her current brood received enough energy to survive and got the chance to reproduce themselves (Davies et al. 2012). Controlling the feeding situation at the nest may also have been a way for the female to reduce a potential family conflict between the nestlings, and prevent the oldest nestling from monopolizing prey items (Sonerud et al. 2013). This would also increase her future potential fitness, since the whole brood would get a better chance of survival. The situation at Isnes, where the youngest nestling died, assumingly due to starvation or siblicide caused by starvation (cf. Forbes 1991), especially supports this assumption. The surviving nestling had no within brood competition, and fed independently for the first time on day 34, i.e. quite some time earlier than at the other nests. Another possibility is a sexual conflict between the male and the female, where the latter attempted to minimize the foraging costs for herself by exploiting prey items delivered at the nest, at the expense of her mate (Sonerud et al. 2013). These potential family conflicts may all occur at the same time (Sonerud et al. 2013).

Partial prey consumption prior to delivery

The probability that a prey item had been eaten at prior to being delivered at the nest was best explained by type of prey species, i.e. prey family. Perch species were less likely to be eaten at than other prey, while mackerels were more likely to be eaten at. A male may choose to feed on a prey item before delivering it at the nest in order to reduce the costs associated with transport (Rands et al. 2000). If this were the actual reason for consuming parts of a prey before transport to the nest I would however expect the model including prey body mass to be the best fit in the analysis, as the net energy gain would vary with prey body mass when corrected for transport costs. Also, all prey types were delivered at the nest in a wide range of masses, so the effect of prey family should not be significant if reduction of transport costs were the reason.

A male may also choose to feed on a prey prior to delivery simply because he has to feed on something, and this way he also had the power to allocate the prey between himself and his mate and nestlings (cf. Sonerud et al. 2013). He may have eaten the front parts because that is the easiest and most natural way to handle a prey item. The same pattern has been seen in the golden eagle; it started feeding on the head of mammalian prey that were not swallowed whole and on the breast of avian prey (Grønsdal 2012). In this case I would however expect the model only including the random effect to be the best effect, as the male would be equally likely to feed on all types of prey, regardless of prey body mass and type. Alternatively, I would expect the model including prey body mass to have a significant effect, as small prey are so quick to eat (Slagsvold & Sonerud 2007) that they are not worth sharing, or even transporting (Sonerud 1992), compared to larger prey.

Another possible explanation is that the flesh on the front parts of the mackerel are of particularly high energetic value while the front parts of perch are of particularly low energetic value compared to the other three most commonly delivered prey types. Feeding primarily on the mackerels and rarely on perches would then give the male the highest energy intake per time unit. It may have been particularly important for the male to feed upon the most energetic prey he captured, as he was in a hurry to provide enough food for his mate and nestlings, and thus had to return quickly to the nest, and then back to the hunting site (Slagsvold & Sonerud 2007). However, perch and pike contain 359 kJ and 353 kJ per 100 g, respectively, while Atlantic mackerel contains 1214 kJ per 100 g (Matvaretabellen 2016). Thus, based on the energy content of mackerel compared to pikes and perches, my explanation may seem likely, but it does not explain why perches had a lower probability of being eaten at prior to being delivered at the nest compared to pikes.

The male may also have assessed each prey item according to the nestlings' ability to feed upon different types of prey at a given time throughout the nestling season, as in the Eurasian kestrel (Steen et al. 2010). I would however expect that delivered prey body mass, as well as nestling age, would be important explanatory variables in the model selection if this were actually the case, since the skin and bone structures generally are more difficult to ingest in larger prey than smaller prey (Slagsvold et al. 2010). The average estimated perch size was indeed considerably smaller than the average estimated carp size, but did not differ much from the average estimated sizes of the other commonly delivered prey types. Moreover, I would think that perches were more difficult to ingest for the nestlings, both when receiving assistance from the female and when feeding unassisted, due to their spikes and rough skin (Nielsen 2011).

Given that the assumption that the perch is actually harder to ingest than the other prey types is actually correct, the handling time of a perch would however have given the male the lowest energy gain per time unit. Based on optimal foraging theory (Stephens & Krebs 1986), and the assumption that the male was in a hurry in order to return to the nest to provide food for the female and nestlings, and then back to the hunting site (Slagsvold & Sonerud 2007), he may not have been able to afford to spend time on eating less profitable prey. The female, on the other hand, was bound to the nest anyway, at least for the first part of the nestling period, and may have more time to handle time-consuming prey, such as the perch. When the nestlings started to feed independently they were also more tightly bound to the nest than the male, and may have afforded to spend more time on prey handling, as long as it meant that the male could return with a new prey more quickly. This prey allocation would then maximize their net gain of energy per time unit.

Decapitation of prey prior to delivery

The probability that a prey item had been decapitated prior to being delivered at the nest was best explained by the model including prey family, while estimated prey body mass was a significant explanatory variable in the second set of analyses that included estimated prey mass for all prey deliveries at the nest. Perch species were less likely to be decapitated prior to being delivered at the nest than the other prey types in the first set of analyses, while the probability that any prey had been decapitated prior to delivery at the nest increased with increasing prey body mass in the second set of analyses. The effect of prey body mass on prey preparation in other raptors is well documented, e.g. for the Eurasian kestrel (Steen et al. 2010).

Larger prey are generally harder to handle, both due to rougher skin and larger bone structures (Slagsvold & Sonerud 2007). A fish head, as well as the heads of other vertebrates, is especially hard and bony due to the cranium, and probably less suitable for the nestlings to swallow compared to the rest of the fish, even when the female dismembered the prey item for them (cf. Steen et al. 2010). The male also had to eat something, and exploiting a resource that he had already captured, but that the nestlings could not handle anyway, may have been a way of reducing the time spent searching for prey (Ydenberg 1994). He was also able to return to the nest site more quickly, as he did not have to capture separate prey items for himself. At the same time, handling costs would be reduced for the nestlings since they would receive parts of the prey that they could utilize more easily.

I assume that the male was time-restricted, since he first had to provide both the female and the nestlings with food for a long period, and thereafter mainly the nestlings until they became independent (Slagsvold & Sonerud 2007). He therefore probably had limited time to self-feed, and time-consuming prey may not have rewarded him a high enough intake rate. Assuming, as earlier, that perches are time-consuming to feed upon due to their spikes and rough skin, the male may not have been able to spend his time feeding upon this prey type. He may therefore have chosen to rather eat the energy-rich heads of the other prey types, which are assumingly easier to handle. The female, on the other hand, was more tightly bound to the nest, and had better time to process prey items before feeding the nestlings. After the nestlings started to ingest prey unassisted, perches may have been a challenging prey, but nestlings were also more tightly bound to the nest, and had more time for prey handling compared to the male.

4.4 Feeding effort

The amount of prey received per nestling per monitored hour block decreased slightly throughout the nestling season. I had expected the opposite, namely an increase in feeding effort, either as the nestling grew older or as an effect of season, since the two variables are assumingly closely correlated. The decrease was probably due to the nestlings receiving some of the prey items outside the nest after fledging, so that these items were not recorded, and the amount of food received was underestimated. The analysis including only the amount of prey received per nestling per monitored hour block before the first nestling fledged the nest showed no effect of either season or nestling age. This supports the explanation that the decrease in the first analysis was caused by some prey deliveries taking place outside the nest, and therefore not recorded.

The female also fed off the prey items delivered by the male at all the nests, but this was not taken into account in the analyses. The amount of food received per nestling per monitored hour block is therefore overestimated, especially in the beginning of the nestling season when the female was constantly tied to the nest. If the amount of food eaten by the female at the nest were excluded, the predicted feeding effort curve may have been lower in the beginning of the nestling season when the nestlings were very small, with a positive slope until they reached their maximum growth rate, as shown for the Eurasian kestrel (Steen et al. 2012).

As the nestlings grew and became less dependent on the female for keeping warm and dismembering of prey, she became more able to fish for herself and the nestlings. There were however few observations of the female delivering prey items to her young at the nests in my study. One theory is that the parents have strict sex-specific tasks, even after the first part of the nestling season where the nestlings depend on her warmth (Cramp & Simmons 1979). The female may have stayed close to the nest to protect the nestlings from potential predators, such as the golden eagle (Cramp & Simmons 1979) and the Eurasian eagle owl (*Bubo bubo*), except when she was fishing for herself. I never observed the nestlings alone during the field season. When the female flew off, assumingly to fish for herself, the male always took her place on a branch close to the nest and the nestlings (pers. obs.).

Another possible explanation is that there was a conflict between the parents over how much each of them should provide for their nestlings (Trivers 1972, Davies et al. 2012). The female may have refrained from fishing for the nestlings, in order to reduce the costs of provisioning, and save her own energy (Sonerud et al. 2013). As long as the male alone was able to provide a sufficient amount of prey for the nestlings, this may increase a female's fitness in the long run. If she is in better condition by the end of the nestling season, she has a better chance of surviving the winter migration and returning to the breeding area the next season. The female at Isnes contributed with more prey items than the females at the other nests. Since the nest was located right next to the water, the costs of transport were potentially very low. She often delivered small prey items (pers. obs.) and it seemed like she just dove down and caught a prey item when she happened to spot something from the nest or from her perching branch. A similar trend has been seen in the Eurasian kestrel, where the female provisioned all the insects delivered at the nest, while the male only provisioned larger prey types (Løw 2006, Sonerud et al. 2013). If this was actually the case in the osprey, the costs of time spent searching were very low, and the net energy gain was probably positive even though small fish have lower energetic value than larger fish. Furthermore, the youngest nestling at the nest at Isnes died before fledging, believed due to starvation or to siblicide caused by starvation (cf. Forbes 1991). The male's insufficient effort to provide for the nestlings may have forced the female to contribute relatively more than the females at the other nests, in order to maximize her fitness through the survival of the remaining nestling. Females adjusting their provisioning effort according to the prey delivery rate of their mate have been reported in other raptors, e.g. in the Tengmalm's owl (Eldegard & Sonerud 2010).

Seasonal distribution of prey items

Carps, perches and pikes were all delivered regularly, but showed a weak decrease in the daily number of deliveries at the nest throughout the nestling season. This weakly declining pattern fits well with the curve for feeding effort throughout the season. Nordbakke (1974, 1980) suggested that freshwater bream was mainly delivered early in the nestling season, due to its spawning in shallow water during this period (Froese & Pauly 2016b). In this study, however, freshwater bream was delivered at the nest throughout the nestling season, together with other carp species. Thus, this species seemed to be equally available throughout the nestling season.

The lack of pikes and perches among prey delivered at the nest during the first eight days of monitoring may have been an effect of season. This does however seem unlikely, since pikes are highly territorial (Froese & Pauly 2016e), and since both pikes and perches locate in shallow and warmer waters in order to maximize their growth rate (Froese & Pauly 2016e,f). Hence, there is no reason to believe that these two prey species were less available in the very beginning of June than 8-9 days later. Another explanation would be that the osprey male delivered different types of prey at the nest as a response to nestling age due to the nestlings' ability to ingest different types of prey as they grew older (Steen et al. 2012), in the same way as the male would make decisions on how to handle different types of prey prior to delivery at the nest. Both pikes and perches have a pretty coarse body with rougher skin and more bones than other prey types, and may therefore have been very difficult for newly hatched nestlings to feed upon. Yet another explanation would be that the lack of these species among the prey delivered was a coincidence, because only one camera was running at the time due to technical problems.

I observed that flounders were delivered at the same rate throughout the nestling season. Thus, the delivery rate of flounders at the nest did not follow the declining pattern of feeding effort, which would be expected assuming that the male osprey adjusted his feeding effort by number of prey items delivered rather than adjusted prey body mass of each item delivered. One possible explanation is that the male osprey delivered flounders more frequently at the nest relative to other prey types once the nestlings became able to ingest this prey type unassisted (Steen et al. 2012, Sonerud et al. 2013) Flounders have such a slim cross section that they might have been easier for the nestlings to peck through than other prey types. After the nestlings had fledged and started to retrieve prey items outside the nest, flounders seemed to be delivered at the nest to a greater extent than other prey. The flounders delivered at the nests in my study were often fairly large, and they were often alive upon delivery (pers. obs.). A flounder is also pretty floppy, so it might have been hard for an inexperienced nestling to handle it while perching on a branch, compared to when perching in the nest.

Mackerels were also delivered at the same rate throughout the nestling season, and did not follow the declining pattern of the feeding effort analysis. As for flounder species, mackerels seemed to be delivered at the nests to a larger extent than other prey species after the nestlings fledged. Also the mackerels were often alive upon delivery, and their agility might have made them hard for inexperienced nestlings to handle while perching on a branch, compared to while perching in the nest.

4.5 Possible biases

The results of this study should be interpreted with some caution, mainly because all the four monitored nest sites were located in a restricted area. Ospreys around the world forage upon a wide range of prey species (Hagen 1952, Nordbakke 1974, 1980, Häkkinen 1978, McLean & Byrd 1991), and behavior and decision making connected to foraging and prey allocation may therefore be expected to show corresponding levels of spatial variation. Human errors in both species determination and size estimation may have occurred, even when the visualization on the video was good. Periods with poor visualization and poor camera connection caused a loss of data in some periods during the study. However, video monitoring is both cost saving and time saving compared to other methods, where human errors may also occur (Steen 2009, Cox et al. 2012). The statistical methods used to analyze the material may also have forced the data into a pattern that is not an actual biological response, but rather a coincidence. Similar studies should be conducted to increase the data material, and thus decrease the chances of biased model predictions. Studies of nesting ospreys in different habitats would also provide a more comprehensive understanding of their prey allocation behavior during the breeding season.

I did not correct for the female foraging at the nest in the feeding effort analysis. Therefore, my measure of feeding effort was nothing but a rough estimate of how much food the males delivered at the nests throughout the nestling season. It would however be interesting to quantify how much prey the nestlings consume and how much the female consumes at the nest at a given time during the nestling period, by counting number of bites during feeding.

5 Conclusion

I found that carp species were the most important prey species overall at all the osprey nests. The average delivered prey mass for all prey items was 380 g, but the range for estimated prey mass was very wide, and also varied considerably between the different nests. Prey items were delivered at the nests during the hours of daylight, with an especially high probability of delivery in the morning hours and late afternoon. Models including the time of day were the best fit to explain the pattern of deliveries for carps, flounders, perches and pikes, while tide and wind speed were additional important factors for mackerels. Mackerels were mainly delivered in early morning and late afternoon, on days when both tide and wind speed were low during these hour blocks. Especially the effect of wind speed may be of concern, since global climate changes are predicted to induce more frequent and stronger winds. Thus, breeding along the coast, where there is little shelter from the wind may be less favorable in the future, forcing ospreys to settle inland. The male delivered nearly all prey items, while the female stayed at the nest and assisted the nestlings in their feeding even longer than what seemed necessary from the nestlings' point of view. This was probably due to a family conflict, where the female tried to save her energy by foraging on prey items brought to the nest by the male. A large proportion of prey were brought to the nest either decapitated or even more eaten at, and perch species had a lower probability of being partly eaten before delivery at the nest compared with the other species, while mackerels had a higher probability of being eaten at. This was probably due to the high energetic value of the mackerel and the long prey handling time required to forage upon perch species, and the fact that the male was in a hurry to return to the nest site to provide food for the female and nestlings. A major restriction in my study is that I have no way of knowing where the ospreys actually went to fish at a given time. With a GPS tag on the birds combined with video monitoring at the nest one could better investigate the effect of wind and other variables on the ospreys' ability to catch different types of prey, and where it chooses to fish under different environmental conditions. This could also give a better understanding of the osprey's ability to adapt to different environmental conditions.

6 References

Ackerman, S. (n.d.). *Sea and land breezes.* Available at: http://cimss.ssec.wisc.edu/wxwise/seabrz.html (accessed 04.05.2016).

Akaike, H. (1978). On the likelihood of a time series model. *The Statistician,* 27:217-235.

Alabaster, J. S., & Robertson, K. G. (1961). The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)) and perch (*Perca fluviatilis* (L.)). *Animal Behaviour,* 9: 187-192.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6.* Available at: https://cran.r-project.org/web/packages/lme4/index.html

Beaumont, W. R. C., Hodder, K. H., Masters, J. E. G., Scott, L. J. & Welton J. S. (2005). Activity patterns in pike (*Esox lucius*), as determined by motion-sensing telemetry. *Aquatic telemetry: Advances and Applications,* 231-243.

Berge, J., Heggland, K., Lønne, O. J., Cottier, F., Hop, H., Gabrielsen, G. W., Nøttestad, L. & Misund, O. A. (2015). First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic,* 68: 54-61.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach,* 2nd edition. New York, USA: Springer Science & Business Media.

Cox, W. A., Pruett, M. S., Benson, T. J., Chiavacci, S. J. & Thompson III, F. R. (2012). *Development of camera technology for monitoring nests.* Berkeley, CA, USA: University of California Press.

Cramp, S. & Simmons, K. E. L. (1979). *The birds of the Western Palearctic,* vol II. Oxford, England: Oxford University Press.

Darbyson, E, Swain, D. P., Chabott, D. & Castonguay, M. (2003). Diel variation in feeding rate and prey composition of herring and mackerel in the southern Gulf of St Lawrence. *Journal of Fish Biology,* 63: 1235-1257.

Davies, N. B., Krebs, J. B. & West, J. A. (2012). *An introduction to behavioural ecology.* 4th ed. West Sussex, UK: Wiley-Blackwell.

Dennis, R. (2008). *A life of ospreys.* Caithness, Scotland: Whittles Publishing.

Dihle, I. (2015). *Prey selection and prey handling in two raptors during the breeding season as revealed by the use of video monitoring.* Master thesis. Ås: Norwegian University of Life Sciences.

Dyfi Osprey Project. (2013). *Seven things you never knew about ospreys.* Available at:http://www.dyfiospreyproject.com/blog/emyrevans/2013/06/11/seven-things-you-never-knew-about-ospreys (accessed 09.03.2016).

eKlima. (2016). Norwegian Meteorological Institute. Available at: http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39049&_dad=portal&_schema=PORTAL (accessed 12.01.2016).

Eldegard, K. & Sonerud, G. A. (2009). Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proceedings of the Royal Society of London B: Biological Sciences,* 276: 1713-1721.

Eldegard, K. & Sonerud, G. A. (2010). Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl. *Behavioral Ecology and Sociobiology,* 64: 815-826.

Eriksson, L. O. (1978). A laboratory study of diel and annual activity rhytms and vertical distribution in the perch, *Perca fluviatilis,* at the Arctic circle. *Environmental Biology of Fishes,* 3: 301-307.

Erkert, H. G. & Kappeler, P. M. (2004). Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi;* Primates: Indriidae). *Behavioral Ecology and Sociobiology,* 57: 174-186.

Forbes, L. S. (1991). Hunger and food allocation among nestlings of facultatively siblicidal ospreys. *Behavioral Ecology and Sociobiology,* 29: 189-195.

Froese, R. & Pauly, D, editors. (2016a). FishBase. Available at: http://www.fishbase.se/Topic/List.php?group=12 (accessed: 20.02.2016)

Froese, R. & Pauly, D, editors. (2016b). FishBase. Available at: http://www.fishbase.se/summary/Abramis-brama.html (accessed 29.03.2016).

Froese, R. & Pauly, D, editors. (2016c). FishBase. Available at: http://www.fishbase.se/summary/Platichthys-flesus.html (accessed

29.03.2016).

Froese, R. & Pauly, D, editors. (2016d). FishBase. Available at: http://www.fishbase.se/summary/Scomber-scombrus.html (accessed at 29.03.2016).

Froese, R. & Pauly, D, editors. (2016e). FishBase. Available at: http://www.fishbase.se/Summary/SpeciesSummary.php?ID=258&AT=pike (accessed 30.03.2016).

Froese, R. & Pauly, D, editors. (2016f). FishBase. Available at: http://www.fishbase.se/Summary/SpeciesSummary.php?ID=358&AT=perch (accessed 30.03.2016).

Gibson, R. N. (1997). Behaviour and the distribution of flatfishes. *Journal of Sea Research,* 37: 241-256.

Google Maps. (2016). Available at: https://www.google.no/maps/ (accessed 24.03.2016).

Grubb, T. G. (1977). Weather-dependent foraging in ospreys. *The Auk,* 94: 146-149.

Grønsdal, E. (2012). *Prey handling by a generalist predator, the golden eagle* (Aquila chryaetos). Master thesis. Ås: The Norwegian University of Life Sciences.

Hagen, Y. (1952). *Rovfuglene og viltpleien.* Oslo, Norway: Gyldendal Norsk forlag.

Häkkinen, I. (1978) Diet of the osprey *Pandion haliaetus* in Finland. *Ornis Scandinavica,* 9: 111-116.

Intergovernmental Panel on Climate Change (2007). *Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, 2007.* Available at: http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html (accessed 18.04.2016).

International Council for the Exploration of the Sea (2013). *Report of the workshop on Northeast Atlantic Mackerel monitoring and methodologies including science and industry involvement.* Available at: http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGESST/2013/WKNAMMM13.pdf (accessed 08.04.2016).

Iversen, S. A. (2002). Changes in the perception of the migration pattern of

Northeast Atlantic mackerel during the last 100 years. *ICES Marine Science Cymposia,* 215: 382-390.

Jepsen, N., Beck, S., Skov, C. & Koed, A. (2001). Behavior of pike (*Esox lucius* L.) >50 cm in a turbid reservoir and in a Clearwater lake. *Ecology of Freshwater Fish,* 10: 26-34.

Kaspari, M. (1990). Prey preparation and the determinants of handling time. *Animal Behaviour,* 40: 118.126.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes.* Berlin, Germany: Kottelat, Cornol and Freyhof.

Lyons, J. & Lucas, M. C. (2002). The combined use of acoustic tracking and echosounding to investigate the movement and distribution of common bream (*Abramis brama*) in the River Trent, England. *Hydrobiologia,* 483: 265-273.

Løw, L. M. (2006). Prey preparation and ingestion rate in breeding Eurasian kestrels *Falco tinnunculus.* Master thesis. Ås: The Norwegian University of Life Sciences.

Matvaretabellen (2016). Available at: http://www.matvaretabellen.no (accessed 12.04.2016).

Mazerolle, M. J. (2016). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC©*. R package version 2.0-4*.* Available at: https://cran.r-project.org/web/packages/AICcmodavg/index.html

McLean, P. K. & Byrd, M. A. (1991). The diet of Chesapeak Bay ospreys and their impact on the local fishery. *Journal of Raptor Research,* 25: 109-112.

Moen, A. G. (2015). *Being at the mercy of their food: What kind of prey do Ural owls* (Strix uralensis) *deliver at the nest in a year with low vole abundance, and when do they deliver what?* Master thesis. Ås: The Norwegian University of Life Sciences.

Nielsen, L. (2011). *Fisker.* 2nd ed. Oslo, Norway: Cappelen Damm.

Nordbakke, R. (1974). *Fiskeørn I sørøstre Østfold.* Cand. real. thesis. Oslo: University in Oslo.

Nordbakke, R. (1980). The diet of a population of ospreys *Pandion haliaetus* in south-eastern Norway. *Fauna norv,* 3: 1-8.

Nygård, M. (2015). *Diet and prey handling at a nest of the golden eagle* (Aquila chryaetos) *in Oppland county, Norway*. Master thesis. Ås: The Norwegian University of Life Sciences.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D & R Core Team (2016). (2016). *nlme: Linear and Nonlinear Mixed Effects Models.* R package version 3.1-127. Available at: https://cran.rproject.org/web/packages/nlme/citation.html

Pita, R., Mira, A. & Beja, P. (2011). Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. *Animal Behaviour,* 81: 1023-1030.

R Development Core Team. (2015). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for statistical computing. Available at: https://www.r-project.org.

Rands, S. A., Houston, A. I. & Gasson, C. E. (2000). Prey processing in central place foragers. *Journal of Theoretical Biology,* 202: 161-174.

Rask, M. (1986). The diet and diel feeding activity of perch *Perca fluviatilis* L., in a small lake in southern Finland. *Annales Zoologici Fennici,* 23: 49-56.

Reebs, S. G. (2003). Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries,* 12: 349-371.

SAS Institute (2012). JMP® Pro version 10.0. SAS Institute Inc.

Schnurre, O. (1956). Ernährungsbiologishe Studien an Raubvögeln und Eulen der Darsshalbinsel. *Beitr. Vogelkunde,* 4: 236-239.

Schnurre, O. (1961). Zur ernährung des Fischadlers. *Beitr. Vogelkunde,* 7: 284-291.

Se havnivå. (2016). The Norwegian Mapping Authority. Available at: http://kartverket.no/en/sehavniva/Lokasjonsside/?cityid=9000024 (accessed: 12.01.2016).

Slagsvold, T. & Sonerud, G. A. (2007). Prey size and ingestion rate in raptors: Importance for sex roles and reversed sexual size dimorphism. *Journal of Avian Biology,* 38: 650-661.

Slagsvold, T., Sonerud, G. A., Grønlien, H. E. & Stige, L. C. (2010). Prey handling in raptors in relation to their morphology and feeding niches. *Journal of Avian Biology* 41: 488-499.

Sonerud, G. A. (1992). Functional responses of birds of prey: biases due to the load-size effect in central place foragers. *Oikos,* 63: 223-232.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2013). Size-biased allocation of prey from male to offspring via female: family conflicts, prey selection, and evolution of sexual size dimorphism in raptors. *Oecologia,* 172: 93-107.

Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G.-H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., Skouen, S. K., Asakskogen, E., Johansen, H. M., Johnsen, J. T., Karlsen, L. I., Nyhus, G. C., Røed, L. T., Skar, K., Sveen, B.-A., Tveiten, R. & Slagsvold, T. (2014a). Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. *Behavioral Ecology*, 25: 762-772.

Sonerud, G. A., Steen, R., Løw, L. M., Røed, L. T., Skar, K., Selås, V. & Slagsvold, T. (2014b). Evolution of parental roles in raptors: diet determines role asymmetry in the Eurasian kestrel. *Animal Behaviour* 96: 31-38.

Steen, R. (2009). A portable digital video surveillance system to monitor prey deliveries at raptor nests. *Journal of Raptor Research,* 43: 69-74.

Steen, R., Løw, L. M., Sonerud, G. A., Selås, V. & Slagsvold, T. (2010). The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel. *Animal Behaviour,* 80: 147-153.

Steen, R., Løw, L. M. & Sonerud, G. A. (2011). Delivery of common lizards (*Zootoca (Lazerta) vivipara*) to nests of Eurasian kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature. *Canadian Journal of Zoology,* 89: 199-205.

Steen, R., Sonerud, G. A. & Slagsvold, T. (2012). Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (*Falco tinnunculus*). *Journal of Ornithology,* 153: 1087-1099.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory.* Princeton, NJ, USA: Princeton University Press.

Thorsnæs, G. (2016). *Glomma.* Store Norske Leksikon. Available at: https://snl.no/Glomma (accessed: 12.02.2016).

Trivers, R. L. (1972). *Parental investment and sexual selection.* Available at: http://www.roberttrivers.com/Publications_files/Trivers%201972.pdf (accessed 18.04.2016).

Turkart Østfold. (2016). Fredrikstad Kommune. Available at: http://kart.fredrikstad.kommune.no/kartklient/internet/turkartostfold/Klient/ (accessed: 20.02.2016).

Vasek, M. & Kubecka, J. (2004). In situ diel pattern of zooplankton consumption by subadult/adult roach *Rutilus rutilus*, bream *Abramis brama,* and bleak *Alburnus alburnus. Folia Zoologica,* 53: 203-214.

Wirjoatmodjo, S. & Pitcher, T. J. (1984). Flounders follow the tides to feed: evidence from ultrasonic tracking in an estuary. *Estuarine, Coastal and Shelf Science,* 19: 231-241.

Ydenberg, R. C. (1994). The behavioral ecology of provisioning in birds. *Ecoscience,* 1: 1-14.

Appendix 1

Table I: Akaike's information criterion (AICc) model selection of factors that affected the probability of at least one prey item from the carp family being delivered at an osprey nest within an hour block. See table 2 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
3	8	1231.04	0.00	0.28
6	9	1232.88	1.84	0.11
12	9	1232.89	1.85	0.11
9	9	1232.89	1.85	0.11
2	6	1233.29	2.25	0.09
18	10	1234.77	3.72	0.04
21	10	1234.80	3.75	0.04
15	10	1234.81	3.77	0.04
5	7	1235.04	4.00	0.04
8	7	1235.16	4.11	0.04
11	7	1235.18	4.13	0.04
17	8	1236.95	5.91	0.01
20	8	1237.00	5.96	0.01
14	8	1237.10	6.06	0.01
1	4	1269.68	38.63	0.00
7	5	1270.95	39.91	0.00
10	5	1271.17	40.13	0.00
4	5	1271.36	40.31	0.00
13	6	1272.71	41.66	0.00
16	6	1272.73	41.69	0.00
19	6	1273.01	41.96	0.00
26	4	1286.61	55.56	0.00
22	3	1290.09	59.04	0.00
25	4	1290.55	59.50	0.00
24	3	1301.34	62.52	0.00
27	4	1302.83	64.51	0.00

0	2	500.13	70.30	0.00
23	3	500.24	71.78	0.00

Table II: Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item from the flounder family being delivered at an osprey nest within an hour block. See table 2 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
8	7	807.13	0.00	0.10
11	7	807.16	0.03	0.10
17	8	807.43	0.30	0.09
12	9	807.47	0.34	0.09
14	8	807.55	0.42	0.08
9	9	807.64	0.51	0.08
15	10	807.95	0.82	0.07
20	8	807.97	0.84	0.07
5	7	807.97	0.84	0.07
18	10	807.99	0.86	0.07
21	10	808.34	1.21	0.06
6	9	808.44	1.31	0.05
2	6	808.81	1.68	0.04
3	8	809.18	2.05	0.04
10	5	826.48	19.35	0.00
7	5	826.79	19.66	0.00
13	6	826.86	19.73	0.00
16	6	826.89	19.76	0.00
19	6	827.18	20.05	0.00
4	5	827.47	20.34	0.00
1	4	828.47	21.34	0.00
26	4	876.59	69.46	0.00
24	3	877.93	70.80	0.00
27	4	879.51	72.38	0.00
25	4	881.84	74.71	0.00
22	3	884.33	77.20	0.00
23	3	884.76	77.63	0.00
0	2	885.53	78.40	0.00

Table III: Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item from the perch family being delivered at an osprey nest within an hour block. See table 2 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
2	6	503.45	0.00	0.23
11	7	504.31	0.86	0.15
8	7	504.84	1.39	0.12
5	7	505.30	1.85	0.09
20	8	505.90	2.45	0.07
14	8	506.04	2.59	0.06
3	8	506.41	2.95	0.05
17	8	506.67	3.22	0.05
12	9	507.30	3.85	0.03
9	9	507.84	4.38	0.03
6	9	508.30	4.84	0.02
1	4	508.61	5.16	0.02
21	10	508.96	5.51	0.01
15	10	509.05	5.60	0.01
18	10	509.71	6.26	0.01
10	5	509.75	6.30	0.01
7	5	510.26	6.81	0.01
4	5	510.47	7.02	0.01
19	6	511.40	7.95	0.00
13	6	511.63	8.18	0.00
16	6	512.11	8.66	0.00
0	2	512.15	8.70	0.00
22	3	512.51	9.06	0.00
23	3	513.17	9.71	0.00
25	4	513.79	10.34	0.00
24	3	514.04	10.59	0.00
26	4	514.51	11.06	0.00
27	4	514.80	11.35	0.00

Table IV: Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item from the mackerel family being delivered at an osprey nest within an hour block. See table 2 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
14	8	320.61	0.00	0.32
15	10	321.36	0.75	0.22
11	7	321.92	1.31	0.16
12	9	322.75	2.14	0.11
20	8	323.61	3.00	0.07
21	10	324.27	3.66	0.05
8	7	325.64	5.02	0.03
9	9	326.38	5.76	0.02
17	8	326.89	6.27	0.01
18	10	327.46	6.85	0.01
2	6	330.08	9.47	0.00
3	8	330.93	10.32	0.00
5	7	331.52	10.91	0.00
6	9	332.26	11.64	0.00
13	6	340.24	19.63	0.00
10	5	341.14	20.53	0.00
19	6	343.11	22.49	0.00
7	5	345.21	24.60	0.00
27	4	345.28	24.67	0.00
25	4	346.41	25.79	0.00
16	6	346.81	26.20	0.00
23	3	347.17	26.56	0.00
1	4	348.53	27.91	0.00
24	3	349.75	29.14	0.00
4	5	350.29	29.68	0.00
26	4	350.83	30.22	0.00
0	2	354.55	33.93	0.00
22	3	354.93	34.31	0.00

Table V: Akaike information criterion (AICc) model selection of factors that affected the probability of at least one prey item from the pike family being delivered at an osprey nest within an hour block. See table 2 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
4	5	330.18	0.00	0.21
1	4	330.79	0.61	0.15
16	6	332.04	1.86	0.08
5	7	332.06	1.88	0.08
19	6	332.17	2.00	0.08
7	5	332.37	2.20	0.07
10	5	332.53	2.35	0.06
2	6	332.99	2.81	0.05
17	8	333.88	3.70	0.03
20	8	334.05	3.88	0.03
13	6	334.26	4.08	0.03
8	7	334.48	4.30	0.02
11	7	334.69	4.51	0.02
6	9	335.18	5.00	0.02
3	8	336.13	5.95	0.01
14	8	336.35	6.17	0.01
24	3	336.71	6.53	0.01
18	10	337.00	6.83	0.01
21	10	337.17	7.00	0.01
9	9	337.63	7.45	0.00
12	9	337.82	7.64	0.00
0	2	338.23	8.06	0.00
26	4	338.35	8.17	0.00
27	4	338.71	8.54	0.00
22	3	339.22	9.05	0.00
15	10	339.49	9.32	0.00
23	3	340.00	9.83	0.00
25	4	340.84	10.67	0.00

Table VI: Effects in model 3 on the predicted probability that at least one prey item of the carp family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-3.06	0.440	-6.94	<0.001
I(cos(2 * pi * Hour/24))	-0.958	0.182	-5.27	<0.001
I(sin(2 * pi * Hour/24))	-0.227	0.111	-2.04	0.042
I(cos(2 * 2 * pi * Hour/24))	-0.835	0.149	-5.59	<0.001
I(sin(2 * 2 * pi * Hour/24))	0.211	0.128	1.65	0.010
I(cos(3 * 2 * pi * Hour/24))	-0.201	0.128	-1.56	0.12
I(sin(3 * 2 * pi * Hour/24))	-0.245	0.125	-1.96	0.050

Table VII: Effects in model 2 on the predicted probability that at least one prey item of the flounder family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-4.59	0.892	-5.15	<0.001
I(cos(2 * pi * Hour/24))	-1.66	0.257	-6.47	<0.001
I(sin(2 * pi * Hour/24))	-0.425	0.156	-2.72	0.0060
I(cos(2 * 2 * pi * Hour/24))	-0.733	0.178	-4.11	<0.001
I(sin(2 * 2 * pi * Hour/24))	-0.366	0.164	-2.23	0.026

Table VIII: Effect in model 2 on the predicted probability that at least one prey item of the perch family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-4.36	0.408	-10.7	<0.001
I(cos(2 * pi * Hour/24))	-0.807	0.271	-2.98	0.0030
I(sin(2 * pi * Hour/24))	0.00744	0.185	0.0400	0.97
I(cos(2 * 2 * pi * Hour/24))	-0.653	0.224	-2.92	0.0040
I(sin(2 * 2 * pi * Hour/24))	0.0389	0.209	0.186	0.85

Table IX: Effects in model 11 on the predicted probability that at least one prey item of the mackerel family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-4.05	1.02	-3.98	<0.001
I(cos(2 * pi * Hour/24))	0.529	0.404	1.31	0.19
I(sin(2 * pi * Hour/24))	0.558	0.225	2.48	0.013
I(cos(2 * 2 * pi * Hour/24))	-1.39	0.335	-4.16	<0.001
I(sin(2 * 2 * pi * Hour/24))	-0.358	0.291	-1.23	0.22
Tide	-0.0416	0.0133	-3.13	<0.001

Table X: Effects in model 14 on the predicted probability that at least one prey item of the mackerel family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-3.79	1.08	-3.52	<0.001
I(cos(2 * pi * Hour/24))	0.448	0.407	1.10	0.27
I(sin(2 * pi * Hour/24))	0.530	0.227	2.34	0.019
I(cos(2 * 2 * pi * Hour/24))	-1.42	0.337	-4.22	<0.001
I(sin(2 * 2 * pi * Hour/24))	-0.316	0.291	-1.08	0.28
Tide	-0.0354	0.0136	-2.61	0.009
FF	-0.142	0.0797	-1.79	0.074

Table XI: Effect in model 1 on the predicted probability that at least one prey item of the pike family was delivered at an osprey nest within an hour block.

	Estimate	SE	z value	P
Intercept	-5.05	0.758	-6.66	<0.001
I(cos(2 * pi * Hour/24))	-0.892	0.288	-3.10	0.0020
I(sin(2 * pi * Hour/24))	-0.260	0.262	-0.993	0.32

Appendix 2

Table I: Akaike's information criterion (AICc) model selection of factors that affected the probability that the osprey female dismembered the prey rather than the nestlings fed independently, based on the analysis including ”prey family” for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. NA = nestling age, PF = prey family. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
3	3	148.01	0.00	0.91
4	7	152.52	4.52	0.09
2	6	485.38	337.38	0.00
1	2	506.99	358.98	0.00

Table II: Akaike's information criterion (AICc) model selection of factors that affected the probability that the osprey female dismembered the prey rather than the nestlings fed independently, based on the analysis including prey mass for all prey deliveries as explanatory varables. NA = nestling age, PM = prey mass. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
4	4	111.63	0.00	1.00
3	3	170.12	58.49	0.00
2	3	488.25	376.62	0.00
1	2	559.26	447.63	0.00

Table III: Akaike's information criterion (AICc) model selection of factors that affected the probability that a prey item delivered at an osprey nest had been eaten at prior to delivery, based on the analysis including "prey family" for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. NA = nestling age, PF = prey family. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
2	6	596.21	0.00	0.59
4	7	596.97	0.76	0.41
1	2	609.54	13.33	0.00
3	3	610.43	14.22	0.00

Table IV: Akaike's information criterion (AICc) model selection of factors that affected the probability that a prey item delivered at an osprey nest had been eaten at prior to delivery, based on the analysis including prey mass for all prey deliveries as explanatory varables. NA = nestling age, PM = prey mass. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
2	3	605.08	0.00	0.58
4	4	605.71	0.63	0.42
1	2	669.74	64.65	0.00
3	3	669.90	64.82	0.00

Table V: Akaike's information criterion (AICc) model selection of factors that affected the probability that a prey item delivered at an osprey nest had been decapitated prior to delivery, based on the analysis including "prey family" for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. NA = nestling age, PF = prey family. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
4	7	569.03	0.00	0.52
2	6	569.21	0.19	0.48
3	3	586.70	17.68	0.00
1	2	586.88	17.85	0.00

Table VI: Akaike's information criterion (AICc) model selection of factors that affected the probability that a prey item delivered at an osprey nest had been decapitated prior to delivery, based on the analysis including prey mass for all delivered prey. NA = nestling age, PM = prey mass. See table 3 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
2	3	577.15	0.00	0.51
4	4	577.20	0.05	0.49
1	2	647.78	70.63	0.00
3	3	647.80	70.65	0.00

Table VII: Effect in model 3 on the probability that the osprey female dismembered the prey rather than the nestlings feeding independently. Based on the analysis including "prey family" for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae.

	Estimate	SE	z value	P
Intercept	12.2	1.67	7.34	<0.001
Nestling age	-0.246	0.0303	-8.13	<0.001

Table VIII: Effect in model 4 on the probability that the osprey female dismembered the prey rather than the nestlings feeding independently. Based on the analysis including prey mass for all delivered prey as explanatory variable.

	Estimate	SE	z value	P
Intercept	16.7	3.08	5.41	<0.001
Prey mass	0.00877	0.00196	4.47	<0.001
Nestling age	-0.395	0.0630	-6.27	<0.001

Table IX: Effect in model 2 on the probability that a prey item delivered at an osprey nest had been eaten at prior to delivery, based on the analysis including ”prey family” for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. Cyprinidae is the reference level in the analysis.

	Estimate	SE	z value	P
Intercept	-0.0529	0.146	-0.364	0.72
Esocidae	0.321	0.396	0.811	0.42
Percidae	-1.22	0.357	-3.42	<0.001
Pleuronectidae	0.266	0.228	1.17	0.24
Scombridae	0.969	0.401	2.41	0.016

Table X: Effect in model 2 on the probability that a prey item delivered at an osprey nest had been eaten at prior to delivery, based on the analysis including ”prey mass” for all delivered prey items as explanatory variable

	Estimate	SE	z value	P
Intercept	-0.163	0.209	-0.777	0.44
Prey mass	-0.0000600	0.000480	-0.134	0.89

Table XI: Effect in model 2 on the probability that a prey item delivered at an osprey nest had been decapitated prior to delivery, based on the analysis including ”prey family” for the five most important prey families as explanatory variable; Cyprinidae, Pleuronectidae, Percidae, Scombridae and Esocidae. Cyprinidae is the reference level in the analysis.

	Estimate	SE	z value	P
Intercept	0.597	0.250	2.39	0.017
Esocidae	-0.187	0.411	-0.454	0.65
Percidae	-1.59	0.353	-4.51	<0.001
Pleuronectidae	-0.324	0.323	-1.01	0.32
Scombridae	0.381	0.485	0.785	0.43

Table XII: Effect in model 2 on the probability that a prey item delivered at an osprey nest had been decapitated prior to delivery, based on the analysis including ”prey mass” for all delivered prey as explanatory variable.

	Estimate	SE	z value	P
Intercept	-0.259	0.254	-1.02	0.31
Prey mass	0.00177	0.000530	3.34	<0.001

Appendix 3

Table I: Akaike's information criterion (AICc) model selection of factors that affected the estimated feeding effort, i.e. the mass of prey received per osprey nestling at the nest per monitored hour block throughout the nestling period. See table 4 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
3	5	189.62	0.00	0.40
4	5	190.40	0.78	0.27
2	4	191.04	1.42	0.20
1	4	192.02	2.39	0.12

Table II: Akaike's information criterion (AICc) model selection of factors that affected the estimated feeding effort before the first nestling fledged the nest, i.e. the mass of prey received per osprey nestling at the nest per monitored hour block throughout the nestling period. See table 4 in methods for model specifications.

Model no.	K	AICc	ΔAICc	AICc-weight
1	4	117.28	0.00	0.37
2	4	117.49	0.21	0.33
4	5	118.80	1.53	0.17
3	5	119.35	2.07	0.13

Table III: Effect in model 2 on the estimated feeding effort, i.e. the mass of prey each osprey nestling received at the nest per monitored hour block throughout the nestling period. See table 4 in methods for model specifications.

	Estimate	SE	t-value	P
Intercept	1.40	0.0875	16.0	<0.001
Julian date	-0.00290	0.00170	-1.77	0.078

Table IV: Effect in model 1 on the estimated feeding effort before the first nestling fledged the nest, i.e. the mass of prey each osprey nestling received at the nest per monitored hour block throughout the nestling period.

	Estimate	SE	t-value	P
Intercept	1.27	0.101	12.5	<0.001
Nestling age	0.00160	0.00340	0.463	0.65

Table V: Effect in model 2 on the estimated feeding effort before the first nestling fledged the nest, i.e. the mass of prey each osprey nestling received at the nest per monitored hour block throughout the nestling period.

	Estimate	SE	t-value	P
Intercept	1.32	0.104	12.7	<0.001
Julian date	-0.000300	0.00290	-0.0987	0.92

Appendix 4

Table I: Parameter estimates for the seasonal distribution of prey items from the carp family at the osprey nests monitored when corrected for nest ID. Nest ID (Leiret) was the reference in the analysis.

	Estimate	SE	X^2	P
Intercept	0.571	0.163	11.6	0.00070
Julian date	-0.0104	0.00357	8.59	0.0034
Nest ID (Elinborg	-1.17	0.205	44.4	<0.0001
Nest ID (Huseby)	0.0398	0.189	0.0442	0.83
Nest ID (Isnes)	0.563	0.128	19.0	<0.0001

Table II: Parameter estimates for the seasonal distribution of prey items from the flounder family at the osprey nests monitored when corrected for nest ID. Nest ID (Leiret) was the reference in the analysis.

	Estimate	SE	X^2	P
Intercept	-0.983	0.341	9.99	0.0016
Julian date	-0.000821	0.00587	0.0196	0.89
Nest ID (Elinborg	1.88	0.272	73.3	<0.0001
Nest ID (Huseby)	1.28	0.352	14.1	0.0002
Nest ID (Isnes)	-1.43	0.525	10.4	0.0013

Table III: Parameter estimates for the seasonal distribution of prey items from the perch family at the osprey nests monitored when corrected for nest ID. Nest ID (Leiret) was the reference in the analysis.

	Estimate	SE	X^2	P
Intercept	-0.651	0.370	3.41	0.065
Julian date	-0.0146	0.00778	3.60	0.058
Nest ID (Elinborg	-0.274	0.376	0.535	0.46
Nest ID (Huseby)	-1.22	0.624	5.42	0.020
Nest ID (Isnes)	1.29	0.283	24.3	<0.0001

Table IV: Parameter estimates for the seasonal distribution of prey items from the mackerel family at the osprey nests monitored when corrected for nest ID. Nest ID (Leiret) was the reference in the analysis.

	Estimate	SE	X^2	P
Intercept	-7.10	$3.07*10^3$	33.7	<0.0001
Julian date	-0.00253	0.00936	0.0729	0.79
Nest ID (Elinborg	6.79	$3.07*10^3$	39.2	<0.0001
Nest ID (Huseby)	4.42	$3.07*10^3$	0.322	0.571
Nest ID (Isnes)	-15.3	$9.21*10^3$	6.57	0.0104

Table V: Parameter estimates for the seasonal distribution of prey items from the pike family at the osprey nests monitored when corrected for nest ID. Nest ID (Leiret) was the reference in the analysis.

	Estimate	SE	X^2	P
Intercept	-5.66	$2.17*10^3$	13.9	0.0002
Julian date	-0.0199	0.00793	6.71	0.0096
Nest ID (Elinborg	-15.6	$6.52*10^3$	22.4	<0.0001
Nest ID (Huseby)	4.75	$2.17*10^3$	2.09	0.148
Nest ID (Isnes)	5.42	$2.17*10^3$	11.9	0.0006

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